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Front cover: *Serranus pulcher* (Iwamoto & Wirtz, p. 25, fig. 21)

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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A Synopsis of the Eastern and Central Atlantic Combers of the Genus *Serranus* (Teleostei: Scorpaeniformes: Serranidae)

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Combers comprise a group of mostly small, shallow-water, tropical to subtropical reef fishes of the genus *Serranus,* subfamily Serraninae. Only a few of the 32 currently known species attain a size exceeding 25 cm TL and few live at depths exceeding 100 m. Three-quarters of the species are found in the Atlantic, with many fewer in the eastern Pacific (6 spp.) and western Indian Ocean (2 spp.). The highest diversity (14 spp.) is in the western Atlantic, with the eastern Atlantic second (10 spp.). No species is found in more than one of these four areas. This synopsis provides a supplement to the treatment of the group by Heemstra and Anderson (2016) in *FAO Species Identification Guide for Fishery Purpose*. We include three additional species: *S. pulcher* Wirtz and Iwamoto, 2016, and two new species herein described: *S. drewesi* Iwamoto, and *S. inexpectatus* Wirtz and Iwamoto. *Serranus drewesi,* known only from the holotype taken by spear in São Tomé, appears most similar to *S. hepatus* but is distinguishable by it cycloid scales, naked interorbital space, pigmentation pattern on the fins and body, gill-raker count of the first arch, and several other characteristics. The type specimens for *Serranus inexpectatus* are from Angola and Gabon, but we suspect that it occurs elsewhere off West Africa. The type specimen from Gabon is that reported by Poll (1954) as *Paracentropristis heterurus*; the excellent illustration in Poll's work has been used erroneously by others as representative of *S. heterurus*. DNA evidence suggests that *S. inexpectatus* is sister to a clade that includes *S. heterurus* and *S. pulcher.* The three are closely similar but each can be distinguished by a combination of pigmentation pattern and meristic and morphometric characteristics. Descriptions, photographs, and a key to the species are provided for the eastern Atlantic species

The genus *Serranus* Cuvier, 1817 has long been a catch-basket for a variety of small to medium-sized fishes in the subfamily Serraninae, family Serranidae. They are frequently referred to as Combers or Dwarf sea basses. Most species are colorful and easily kept in aquariums, thus their popularity among aquarists and divers. Some species are important components of artisanal fisheries. Nelson (2006:346) listed 11 genera as examples of the subfamily, although Meisler (1987), in a comprehensive unpublished revision of the serranines, provided a classification, based on a cladistic analysis, that included only 10 genera, excluding two of the genera Nelson listed and adding *Mentiperca* Gill, 1862. Robins and Starck (1961) in their revision of western Atlantic *Serranus* recognized only two subgenera, *Serranus* and *Paracentropristis* Klunzinger, 1884, but Meisler (1987) recognized four subgenera: *Serranus*, *Paracentropristis, Dules* Cuvier, 1829*,* and *Prionodes* Jenyns, 1842.

Only species of the subgenera *Serranus* and *Paracentropristis* are known from the eastern Atlantic: one species is endemic to the central Atlantic islands of Ascension and St. Helena and nine valid species are known from the eastern Atlantic. Heemstra and Anderson (2016) recorded eight species of *Serranus* in their chapter on the Serranidae in the revised edition of the FAO series *The Living Marine Resources of the Eastern Central Atlantic* (Carpenter and Angelis, 2016), including among them *Serranus africanus* (Cadenat, 1960), which we here treat as a member of the genus *Chelidoperca*. Williams and Carpenter (2015:287), in describing *Chelidoperca santosi* from the Philippines, did not include *C. africana* in their list of the seven nominal species of the genus, noting that "an eighth nominal species from the Atlantic has been reassigned to the genus *Serranus*." That eighth species is presumably *C. africana.* Heemstra and Anderson (2016) did not include *S. pulcher* Wirtz and Iwamoto, 2016, because it was described after their FAO publication. We describe herein one new species from the Gulf of Guinea island of São Tomé and a second from Angola and Gabon. Thus, a total of ten species of *Serranus* is now known from the eastern and central Atlantic. Four of the ten have distributions extending into the Mediterranean Sea, and *S. cabrilla*, with the widest range, is also recorded from the Black Sea, as well as in the Red Sea where it apparently arrived as an invasive species (Norman 1927; Tortonese 1954).

Heemstra and Anderson's (2016) contribution to the FAO *Species Identification Guide to the Marine Resources of the Eastern Central Atlantic* includes descriptions and illustrations of seven *Serranus* species plus *Chelidoperca africana*. We have incorporated information from that work and added additional information based on our findings. For some species, new collections have extended their geographical ranges; extensive diving observations by the second author have increased our knowledge of the life history and habits of the species. Color photographs of living and fresh specimens, of which we provide many, are of particular value in showing the wide variation in color pattern found in some species. *Chelidoperca africana* Cadenat, 1960, is included in the key because it is frequently treated as a member of the genus *Serranus.*

Material and Methods

Specimens examined are deposited in the California Academy of Sciences (CAS and CAS-SU), the National Museum of Natural History (USNM), the Natural History Museum of Los Angeles County (LACM), Royal Belgian Institute of Natural Sciences (RBINS), South African Institute of Aquatic Biodiversity (SAIAB), Stuttgart Natural History Museum (SMNS), the Zoologische Staatssammlung, München (ZSM).

Anatomical terms and abbreviations, and methods for making measurements and counts follow those described in numerous ichthyological texts, including Hubbs and Lagler (1964), Smith and Heemstra (1986), and the various FAO species identification guides for fishery purposes (e.g., Carpenter 2002:603-610; 2016:1513–1518). The last ray of the dorsal and anal fins is usually split to the base and is counted as one ray; almost all eastern Atlantic species have seven soft rays in the anal fin, although *S. atricauda* is an exception with a normal of eight, *S. hepatus* has six or seven, and *S. drewesi* has six. Pectoral-fin ray counts include the small splintlike uppermost ray. Pored lateral-line scales are taken to the caudal-fin base and do not include those on the caudal fin itself; the value of lateral-line and circumpeduncular scale counts as applied to *Serranus* was discussed by Robins and Starck (1961:260). Gill-raker counts are from the first arch and include all rudiments; counts of the upper arm are separated by a plus sign (+) from those of the lower arm, the raker whose root spans both arms is included in the count of the lower arm. Meristic characters provided in the text but not in the tables are ours and do not include counts from the literature that are extralimital to the ranges we recorded. The descriptions of color patterns are based on numerous underwater photographs by the second author and others (see Acknowledgments) as well as freshly captured specimens. The term stripe is used for narrow horizontal to diagonal markings, whereas band, bar, and saddle refer to more-or-less vertical markings. Sizes given in the Specimens Examined sections are in standard length (SL) and head length (HL); those in the text under Size are for total length (TL). We have made liberal use of published descriptions and records for this study and have made an effort to cite all appropriate references. The reader is referred to the *Checklist of the fishes of the eastern tropical Atlantic* (Quéro et al. 1990) for extensive synonymies. Full references for scientific names are provided in Eschmeyer's *Catalog of Fishes* (2018) online at <*http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp*>.

Taxonomy

Genus *Serranus* Cuvier, 1817

Type species *Perca cabrilla* Linnaeus, 1758 (as designated by ICZN, Official List, Opinion 93).

Diagnosis.— D X,12–15; A III,6–8, usually 7; P 12–18; V I,5; BR 7; vertebrae 10+14. Dorsal fin undivided, spinous and soft rays broadly united; caudal fin truncate, emarginate, or moderately forked, with 17 principal rays (15 branched); supramaxilla absent; teeth on vomer and palatines, none on tongue. Opercle with two or (usually) three flattened spines, the lowermost sometimes obscure or undeveloped; central spine largest and directed horizontally. A spinous-edged suprascapular scale present. Scales mostly ctenoid, but some species have cycloid scales on head or trunk and *S. drewesi* n. sp. has all scales cycloid; interorbit, occiput, upper part of postorbital region and interopercle variously scaled or naked; lateral line complete, with pored scales; maxilla naked. Species probably all synchronous hermaphrodites. Most species small, less than 20 cm TL, but a few attain about 40 cm TL (mostly from Robins and Starck, 1961:261).

Remarks.— Members of the genus are found on both sides of the Atlantic (including the Mediterranean and Black Seas, and in the Red Sea as an invasive), in the tropical eastern Pacific, and in the southwestern Indian Ocean off South Africa. The highest diversity is found in the western central Atlantic (14 spp.), followed by the eastern Atlantic (10 spp.), the eastern Pacific (6 spp.), and the Indian Ocean (2 spp.). The species are apparently endemic to each region, as no species is found in more than one region. Kuiter (2004:80) listed 30 described species of *Serranus* and two undescribed species, but one of the described species he listed is *Chelidoperca africana* Cadenat, 1960, which we consider as the only member of *Chelidoperca* in the Atlantic. *Chelidoperca* is otherwise known from 10 other species of the Indo-West Pacific (Matsunuma et al. 2018). Table 1 lists 32 species of *Serranus*, based on Kuiter (loc. cit.) and our findings.

Robins and Starck (1961) comprehensively treated the western Atlantic species of *Serranus* and provided valuable additional information on the genus, its included species, and relationships to other serranines; they also gave excellent descriptions of three eastern Atlantic species for which they had specimens. They considered that the anal fin-ray count of III,7 was the common number, but we found that our two specimens of *S. atricauda* had III,8, as did one of our specimens of *S. scriba* (CAS-SU 20897). Meisler (1987:152) stated that, *S. atricauda* "is the only *Serranus* species to have exclusively eight anal rays." Heemstra and Anderson (2016:2410) gave the anal fin-ray count for *S. hepatus* as III,6 or 7, but seven of our 10 specimens of that species had a count of III,7; the other had III,6. The holotype and only specimen of *S. drewesi* n.sp. has an anal fin-ray count of III,6.

It is regrettable that Martin R. Meisler's Ph.D. dissertation (1987) was never published inasmuch as it is a comprehensive revisionary work on the group, based on study of most of the species of *Serranus* and *Mentiperca* (as well as numerous other serranid genera) and a phylogenetic analysis using a variety of osteological, myological, and external characters. It contains a wealth of original information not elsewhere available and the bibliography is comprehensive to that time.

***Serranus* (*Paracentropristis*) *accraensis* (Norman, 1931)**

Figure 1

Neanthias accraensis Norman, 1931 (holotype BMNH 1930.8.26.28; Accra, Ghana). Fowler 1936:1292–1293, fig. 550; 1357 (compiled). Poll 1954:78–81, fig. 23 (Gabon to Angola; 50-75 m).

Novanthias accraensis: Whitley 1937:122 (replacement name for genus *Neanthias*, preoccupied by *Neanthias* Rye, 1881).

Serranus sanctae-helenae (non Boulenger 1895): Poll 1948:225.

Serranus accraensis: Robins and Starck 1961:259. Smith 1981:703-704. Heemstra and Anderson 2016:2406.

Diagnosis.— D X,12; A III,7; P 16–17; V III,7; gill rakers 6-8+13–15 (20–23 total); pored lateral-line scales 43–48; circumpeduncular scales 22–23. Upper lobe of caudal fin ending in a short filamentous streamer produced beyond tip of lower lobe. Rim of tube-like anterior nostril elevated to a flap posteriorly and fringed at tip. Two diagonal bluish stripes on side of head, one behind eye, the other below eye running from snout to margin of opercle. A faint broad stripe below lateral line, usually broken into a series of 4–7 bands or blotches, the bands (often indistinct) extending from dorsal profile to a mid-lateral position; the band or blotch below the 7th and 8th dorsal spines usually darkest, although that on caudal peduncle forming a dark blotch in some specimens.

Description.— Body compressed and moderately slender; greatest depth under origin of dorsal fin about one-third SL; head length 35–37% of SL. Snout rather short, its length subequal to orbit diameter; dorsal profile of snout with mouth tightly closed attaining a slope of approximately 45 degrees from the horizontal; the profile leveling off over orbits and rising slightly over body; the ventral profile of body forming a gentle uniform curve from lower jaw to base of caudal fin. Jaws equal, the upper jaw extending almost to vertical through midorbit. Anterior nostril a short tube, the posterior rim with 4–6 slender fingerlike cirri. Three short flat spines on opercle, the uppermost scarcely visible below the overriding scale, the second best developed, the third small and inconspicuous. Preopercle margin armed with small serrations along entire free margin in adults, but reduced or absent ventrally in young; spines at angle usually slightly enlarged.

Premaxillary teeth with two short canines in a cluster of teeth near tip of jaw, followed by smaller conical teeth posteriorly, and flanked medially by a narrow inner band of small teeth. Dentary teeth composed of 4–6 short recurved and spaced canines interspersed with much smaller teeth in one row. Vomer with cluster of small teeth in broadly V-shaped patch. Palatine teeth all small, in an elongated lens-shaped band.

Body scales large, ctenoid, covering most of body; scales absent on top of head, snout, suborbital region, jaws, gular and branchiostegal membranes, interopercle bone, and in larger specimens, broad outer margin of preopercle, a narrow area behind orbit, and lower margin of subopercle. No scales on dorsal and anal fins, but small scales present at bases of pectoral, pelvic, and caudal fins.

First 4–6 spines of dorsal fin graduated, the spines following subequal; the segmented rays slightly higher, forming a slight notch in profile of dorsal fin. Anal-fin spines graduated, the first less than half length of second and third spines; segmented rays longer than spines, the last three or four segmented rays longest. Pectoral fin broad-based, its origin slightly behind that of pelvic fin and about on same vertical as origin of dorsal fin, its distal tip extending close to or over origin of anal fin. Tip of second pelvic-fin ray developed into a short filamentous streamer. Caudal fin lunate, upper caudal lobe with a short filamentous streamer and longer than lower lobe.

***Color in fresh specimens*:** (Fig. 1) Ground color light gold to bronze, overlain dorsally with

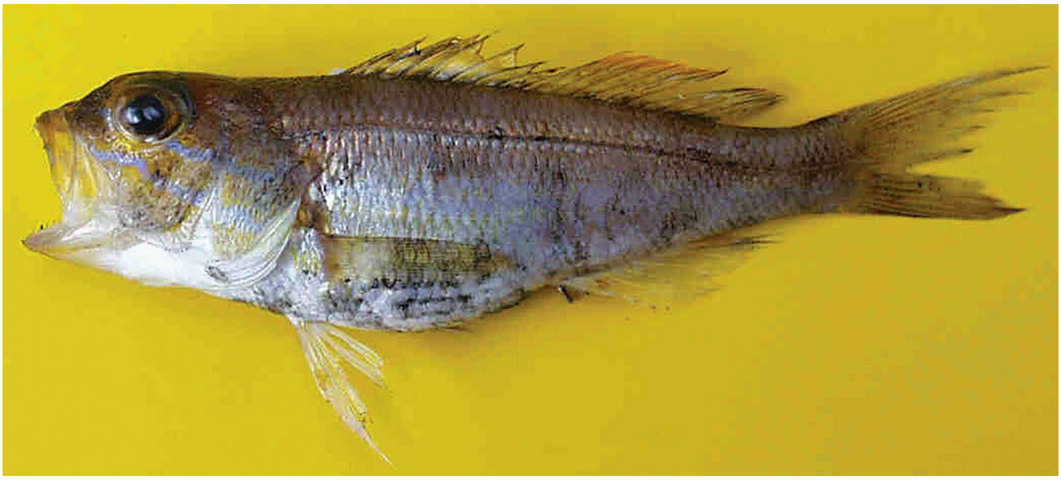

FIGURE 1. *Serranus accraensis*. A fresh 14 cm TL specimen from West Africa, taken by the R/V *Dr. Fridtjof Nansen* in 47 m. Photograph by Oddgeir Alvheim.

brownish hue and darker scale outlines; silvery to white below, ivory-white on gular and branchiostegal membranes, chest (including cleithrum and pectoral-fin base), and belly to origin of anal fin. Five to seven indistinct broad olive-green bands descend from dorsum to midlateral line where they become darker and form blotches, the blotch below dorsal spines VI to VIII usually darkest and largest, those more posterior smaller and fainter, although that on caudal peduncle often forming prominent dark blotch. Two characteristic blue stripes on side of head, the upper running at a shallow diagonal from the posteroventral corner of orbit to margin of gill cover between second and third opercular spines, the lower stripe beginning at snout and running below orbit to margin of gill cover. Dorsal fin olive-brown overall, with a clear basal stripe on spinous portion rising posteriorly above a narrow dark base; distally, small clear spots dot darker ground, with a faint orange margin on soft-dorsal portion of fin. Pectoral and pelvic fins faintly yellow; anal fin with golden-yellow stripe midlaterally, clear otherwise; caudal fin olive-brown, darker on ventral lobe; small clear spots along interradial membranes. In preserved specimens: the bluish stripes on head are dark and the midlateral blotches are more prominent; also, three narrow stripes on body become visible: one running along lateral line, ending near where lateral line descends; a second stripe running midlaterally from behind lower margin of fleshy opercular lobe to caudal peduncle; the third running from behind belly at mid-level of pectoral fin and ending above end of anal fin.

Size**:** To about 20 cm TL.

HABITAT AND DISTRIBUTION.— Muddy and sandy bottoms from 25–150 m. Senegal to Angola, São Tomé Island (first record, based on CAS 231616).

REMARKS.— This is a relatively common species in tropical West Africa at depths of approximately 40 to 80 m. Poll (1954: 78-79) recorded 180 specimens collected at 10 localities between the equator off Gabon and the Congo River in northern Angola. The first author encountered the species infrequently during *R/V Nansen* surveys off Senegal, Ghana, São Tomé e Príncipe, and Angola.

SPECIMENS EXAMINED (9 spec.; 8 from *R/V Dr Fridtjof Nansen* [*DFN*] surveys collected by the first author).— **Senegal:** CAS 234557 (1 spec., 88.6 mm SL); 15°19.1′N, 16°55.5′W; 53–50 m; *DFN* Survey 2012-04-04, sta.98; 28 May 2012. CAS 234896 (1, 129 mm SL); 14°29.09′N, 17°20.2′W; 58–57 m; *DFN* Survey 2012-04-04, sta.89; 27 May 2012. **Ghana**: CAS 231637 (2, 89.5–93.6 mm SL); 5°37.06′N, 0°34.47′E, 45–46 m; *DFN* Survey 2010-04-04, sta 5; 1 May

2010. **São Tomé e Príncipe:** CAS 231616 (1 spec., 101 mm SL); off São Tomé Island, 0°8.46′N, 6°41.42′E, 54-61 m; *DFN* Survey 2010-04-05, sta. 26, 16 May 2010. **Cameroon:** CAS-SU 55584 (1, 118.5 mm SL); Kribi; 2.938408°N, 9.908068°E; collector A.I. Good, 12 Apr. 1940. **Angola:** CAS 222858 (1, 88.5 mm SL); 12°17′S, 13°34′E; 53–57 m; *DFN* sta. 43611, 2 Apr. 2005. CAS 234758 (1, 133.5 mm SL); 12°00.06′S, 13°37.06′E; 73 m; *DFN* sta. 40, 4 Mar. 2007. CAS 224982 (1, 67.6 mm SL); 10°54.91'S, 13°43.7′E; 54–55 m; *DFN* sta. 61, 6 Mar. 2007.

***Serranus* (*Serranus*) *atricauda* (Günther, 1874)**

Figures 2–4

Serranus (*Serranus*) *atricauda* Günther, 1874:230 (Mogador [Essaouira, Morocco]). *Paracentropristis atricauda*: Fowler, 1936:768

Diagnosis.— D X,15–16; P 17; A III,7–8, usually 8; gill rakers 8+14–15(22–23 total); pored lateral-line scales 80-90; circumpeduncular scales about 47. Caudal fin truncate; upper lobe slightly elongated and pointed at tip; lower lobe rounded. Snout, anterior half of suborbital region, top of head, jaws, gular and branchiostegal membranes, most of interorbital, and outer margin of preopercle naked; all fins with small scales on basal portion of rays. Anterior nostril with raised rim, posterior portion of rim elevated into a narrow flap lacking fingerlike fringes. Adults with midlateral series of squarish black blotches, often broken by narrow white vertical bars (but not in yellow morphs, see below). Tips of caudal fin and distal margin of anal fin blackish.

Description.— Head about 2.7–3.0 time in SL; snout pointed, longer than orbit, about 3.8–4.0 in HL; orbit and interorbital space about equal, and about 4–6 times in HL. Body relatively shallow, 3.3–3.5 times in SL, compressed, the dorsal profile gently curved from snout tip to end of tail, ventral profile similarly smooth but less curved. Three flat spines on opercle, the uppermost and lowermost much shorter than middle spine, the narrow opercular flap extending beyond middle spine a distance about equal to length of that spine. Preopercle margin armed with small serrations along entire free margin.

Premaxillary teeth with two or three short canines on outer border of a cluster of teeth near tip of jaw, and one or two larger canines on inner mesial margin of cluster; the anterior cluster tapering to a narrow band posteriorly, flanked by a spaced series of smaller conical teeth. Dentary with moderately wide band of small teeth anteriorly, with two prominent canines at tip; the band narrowing to one or two irregular series of small, spaced canines interspersed with a few large canines near mid-length of jaw. Vomer with small teeth in a broadly V-shaped band; palatine teeth small, in a short narrow band.

First 4–6 spines of dorsal fin graduated, the spines following subequal; 5th or 6th spine longest, their length about equal to distance orbit to angle of preopercle; the soft dorsal slightly higher where it joins spinous dorsal, creating a slight rise but no distinct notch in profile of dorsal fin; longest spine (5th or 6th) about equal to longest segmented ray. Anal-fin spines graduated, the first 44–60% length of second and third spines, which are about equal; segmented rays of anal fin longer than spines, the last three or four segmented rays longest. Pectoral fin broad-based, its origin about on same vertical as origin of dorsal and pelvic fins; distal tips of pectoral and pelvic fins falling well short of anal fin.

Color**:** Adults (Fig. 2) commonly have a white longitudinal stripe on body over anterior half of lateral line, after which the stripe narrows as it continues its horizontal course to the upper margin of the caudal peduncle, while the lateral line descends to a midlateral position; below this white stripe are four or five large, dark, rectangular blocks, each block alternating with a narrow dark vertical band; about five large dark blotches on dorsum below dorsal fin; small dark spots

FIGURE 2. *Serranus atricauda.* Adult from Faial Island, Azores. Photograph by Peter Wirtz.

FIGURE 3. *Serranus atricauda.* Juvenile from Faial Island, Azores. Photograph by Peter Wirtz.

FIGURE 4. *Serranus atricauda.* Adult yellow morph from Cape Verde Islands. Photograph by Reinhold Hanel.

arrayed along ventral border of longitudinal white stripe from behind gill cover to upper margin of caudal peduncle; median fins with numerous pale blue dots, which extend onto caudal peduncle in three horizontal rows; two or three dark oblique stripes on cheek; tips of anal and caudal fins black. Juveniles (Fig. 3) often differ in having a broad white stripe bordered by two black stripes, the upper black stripe extending from tip of snout to base of upper caudal-fin lobe, the lower extending from below eye to base of lower caudal-fin lobe; caudal fin transparent. A photograph of a yellow morph from the Cape Verde Islands (presumably from deep water) (Fig. 4) shows body overall brownish yellow, the dorsal two-thirds darker, the ventral one-third pale whitish. About 15 vertically elongated darker blotches on sides of body, some partially merged with others. Head with yellow stripes, one stripe running from snout tip through eye and onto upper margin of gill cover; another running below eye and bifurcating into two stripes on preopercle; a third stripe along upper margin of maxilla. One or two broader irregular stripes on nape. Dorsal fin yellow overall with dark distal margin on soft dorsal; pectoral fin yellow; pelvic fin mostly blackish, but base and spine pale whitish; anal spine pale, soft rays yellow near base and blackish over most of distal portion; caudal fin mostly yellow with prominent black tips on upper and lower lobes, posterior margin faintly blackish.

***Size*:** Maximum size about 35 cm TL.

HABITAT AND DISTRIBUTION.— Over hard bottoms from the shore to about 90 m; from the Bay of Biscay to Guinea Bissau, including the Azores, Madeira, Canary Islands, Cape Verde Islands, and also in the Mediterranean Sea.

REMARKS.— This is a common species that supports artisanal fisheries in the off-shore islands of the African coast as well as slong the continental coastline from the Bay of Biscay to Mauritania, and also in the Mediterranean Sea. The only record that we know of from the mainland coast of West Africa south of Mauritania is by (Heemstra and Anderson 2016) from off Guinea-Bissau.

SPECIMENS EXAMINED (2 spec.).— **Canary Islands:** CAS-SU 3108 (2, 150–185 mm SL); Canary Is.; collector C.F. Cook.

***Serranus* (*Serranus*) *cabrilla* (Linnaeus, 1758)**

Figures 5–7

Perca cabrilla Linnaeus, 1758 (no locality given).

Paracentropristis cabrilla: Fowler, 1936:1291 (14 spec., 137–325 mm; Madeira, Canaries, Azores).

Serranus cabrilla: Poll 1954:69–72, fig. 19 (17 spec., 79–240 mm; Gabon to s. Angola). Robins and Starck 1961:261–262, figs. 1a, 7c, 8a, 8c (4 spec., Spain and Italy). Quero et al. 1990:704–705 (compiled).

DIAGNOSIS.— D X,13–14; P 14–16; V III,7; gill rakers 6–8+12–16 (18–24 total); pored lateral-line scales 70–77; circumpeduncular scales 36–40. Caudal fin shallowly forked, upper lobe slightly longer than lower lobe, a very short streamer on upper lobe in juveniles, but none developed in adults. Interradial membranes of dorsal and anal fins scaled on basal one-half to one-third. Nape, opercle, cheek, pectoral-fin base and chest scaled.

DESCRIPTION.— Body compressed, width across pectoral fin base about 2 in HL; depth about 3 in SL; head about 2.7–2.8 in SL. Dorsal and ventral profiles gently curved; the snout pointed and longer than orbit diameter; interorbital width (fleshy) slightly greater than orbit diameter; lower jaw projecting beyond upper jaw; maxilla extending to below midorbit. Anterior nostrils with low rims lacking fingerlike fringes or cirri. Opercular spines three, the upper two fairly well developed, the lowermost obscure in adults, but more visible in juveniles. Preopercle margin coarsely serrated, largest spines near angle. Interopercle smooth, (a few imbedded scales in large specimens); snout, interorbit, occiput, suborbit, jaws, gular and branchiostegal membranes naked.

FIGURE 5. *Serranus cabrilla.* Adult from near Hyères, Var, Provence, France. Photograph by Lucas Berenger.

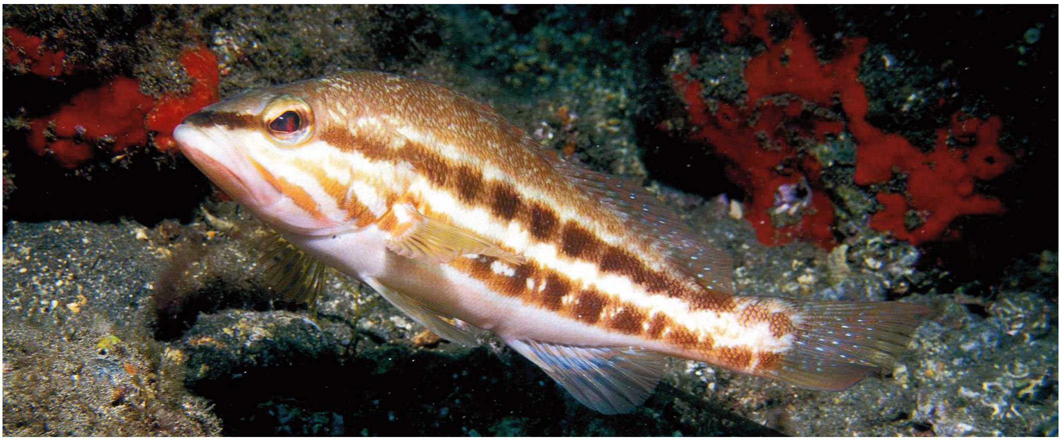

FIGURE 6. *Serranus cabrilla.* Adult from the Canary Islands. Photograph by Rogelio Herrera.

FIGURE 7. *Serranus cabrilla.* Yellow morph from Ivory Coast (4°34′N, 6°37′W), collected by R/V Dr. Fridtjof Nansen by bottom trawl in 81 m. Photograph by Oddgeir Alvheim.

Premaxillary teeth in several irregular rows, the outer enlarged with one or more large canines at anterior end. A single file of enlarged, spaced teeth on dentary, largest teeth midlength on jaw; much smaller teeth interspersed on sides of larger teeth and a cluster of small teeth at anterior end. Vomer broadly V-shaped with small teeth. Palatine teeth all small, in a short to elongate patch.

Scales small, ctenoid, present on sides of head and nape to margin of frontals, but absent on interorbital, snout, suborbital region, jaws, gular and branchiostegal membranes, interopercle bone, outer margin of preopercle, and lower margin of subopercle. Small scales at bases of dorsal, anal, pectoral and caudal fins, and minimally (if at all) on pelvic fins.

First 4–6 spines of dorsal fin graduated, the 6th spine usually longest, the spines following subequal; the soft rays slightly higher, forming a slight rise (but no distinct notch) in profile of dorsal fin. Anal-fin spines much shorter than soft rays, the first spine somewhat more than half length of second and third spines, the last three or four soft rays longest. Pectoral fin broad-based, its origin slightly behind that of pelvic fins and about on same vertical as origin of dorsal fin, its distal tip over anus, slightly behind origin of anal fin. Pelvic fin falling well short of anus. Caudal fin shallowly lunate, almost truncate, upper and lower lobes about equal, but upper lobe with a very short streamer in small juveniles.

***Color*:** (Fig. 5) A series of about nine dark vertical bands along the light brown to reddish body, interrupted in some specimens by two or three white stripes; underside of head and belly mostly white; bands on body reduced to dark lateral blotches in some. Caudal and soft dorsal fins punctated with small bluish dots; in some individuals the basal one-third to one-half of soft dorsal fin dark but distally pale with small bluish spots; tips of caudal fin occasionally reddish (Fig. 6). Posterior margin of caudal fin occasionally blackish but never with black lobes as in *S. atricauda*. Juveniles may be quite different: a white midlateral stripe bordered by two thick black stripes, the upper stripe running from tip of snout through middle of eye to upper margin of operculum onto trunk above midlateral line to upper half of caudal peduncle, the lower stripe from base of pectoral fin to lower half of caudal peduncle; the dark stripes often partially broken into dark blotches. The juvenile color pattern is often very similar to that of *S. atricauda* (compare with Fig. 3), although three juveniles (CAS 234559, 44.4–50.7 mm SL) trawled in 53–50 m off Senegal lacked the prominent dark lateral stripes.

As in many other fish species, *S. cabrilla* specimens from deep water tend to be more yellow (Medioni et al. 2001). In one individual from deeper waters at the Azores (Fig. 7), ground color golden-yellow on flanks, yellowish-orange on head, and brownish to tan on dorsum; four or five metallic-blue longitudinal lines or stripes on body and three diagonal stripes on head, the lowest stripe on head originating on snout and running to preopercle angle onto subopercle; the upper two stripes originating below orbit and terminating at margin of opercle. A fourth diagonal stripe present in some, originating on posterior portion of maxilla and extending a short distance onto preopercle. Fins yellowish; the soft dorsal with dark basal half, the dark bands on body extending onto dorsal-fin rays.

Size: 40 cm TL.

HABITAT AND DISTRIBUTION.— Over hard bottoms from the shore to 450 m; from the British Isles to Angola, including the Azores, Madeira, the Canary Islands, São Tomé Island (based on photo by the second author) and Príncipe Island (first record based on CAS 234287), apparently here and only in deep water at the Cape Verde Islands (Freitas et al., in prep.); also throughout the Mediterranean and into the Black Sea. Its presence in the Red Sea is attributed to invasion from the Mediterranean Sea after the Suez Canal was opened in 1869 (Norman 1927; Tortonese 1954; Meisler 1988:156). Records of the species from South Africa are apparently of the closely similar *S. knysnaensis* Gilchrist, 1904 (Heemstra and Anderson, 2016).

Specimens examined (14 spec.).— **São Tomé e Príncipe:** CAS 234287 (1, 208 mm SL); Príncipe Is., purchased dockside in São Tomé City from fisherman selling catch taken off Príncipe; 7 Apr. 2012. **Senegal:** CAS 234559 (3, 44.4–50.7 mm SL); 15°19.1′N, 16°55.5′W, 53–50 m; *R/V Dr Fridtjof Nansen* CCLME Survey 2012, sta. 98, 28 May 2012. **Ghana:** CAS 234960 (1, 205 mm SL); 5°54.77′N, 1°16.15′E; 94–95 m; *R/V Dr Fridtjof Nansen* Survey 2010.04.04, sta. 1; 30 Apr. 2010. **Cameroon:** CAS 238009 (1, 195 mm SL); collector A.I. Good; 1940. **Italy**: CAS-SU 20933 (3, 142-216 mm SL); and CAS-SU 20933 (3, 142–175 mm SL); Naples; collector E.C. Starks; ca. 1907. CAS-IU 7545 (1, 162 mm SL); Sicily, Palermo; collector P. Doderlein; 1886. **Spain:** CAS-SU 69064 (1, 171 mm SL); Mediterranean Sea; Gibralter, Gibralter Harbor; collector T.H. Work; 12 Aug. 1947. **Red Sea:** USNM 203668 (4, 60–98 mm SL); "Abu Zueima" [*sic*, possibly Abu Zenima, in Egypt]; coll. H. Steinitz, 22 Sept. 1967.

Serranus (*Paracentropristis*) *drewesi* Iwamoto, sp. nov.

Figure 8

Diagnosis.— D X,11; P 14; A III,6; gill rakers 3+11; scales below 1D origin about 5, below 2D 4+1+8 or 9, pored lateral-line scales 44; circumpeduncular scales 1+9+1+10 (21 total). Anterior nostril tubular, rim greatly elevated posteriorly and bearing about 7 or 8 long cirri at tip. Scales all cycloid (except for a hard, sharply spinulated suprascapular scale bone above the upper opening of the gill cover). Caudal fin weakly emarginate, upper and lower lobes about equal. Interradial membranes of soft dorsal and anal fins scaly on basal one-half to one-third. Nape, opercle, preopercle, interopercle, mandibular ramus, pectoral-fin base, and chest covered with cycloid scales. A bold black spot between last three spines and first soft dorsal ray formed above broad black saddle on dorsal half of body.

Description.— Head and body laterally compressed, greatest width of head 6.3 times in SL, greatest body width 5.9 times in SL. Snout pointed, longer than orbit diameter; interorbital space narrow, bony width about 60% of greatest orbit diameter. Orbit about 4 in HL; pupil sharply egg-shaped with pronounced anterior aphakic (lensless) space. Jaws equal; posterior margin of maxilla below middle of orbit. Two broad, flat, weak opercular spines developed, the dorsal spine partially obscured by skin and scales, lower spine more prominent and forming posterodorsal corner of gill cover. Anterior nostril tubular, rim low anteriorly but elevated into a long flap posteriorly, the flap fringed with 7 or 8 long cirri, a few filaments longer than height of flap. Gill opening ventrally extending forward to about vertical passing through hind edge of orbit. Gill rakers relatively short, stout and recurved, the uppermost on lower limb (ceratobranchial) about 1.5 mm in length, the succeeding rakers gradually shorter with last three or so tubercular. About 11 pseudobranchs.

Spinous dorsal fin with middle spines longest, a prominent dip between spinous and soft-rayed portions of dorsal fin; the longest dorsal spine shorter than longest dorsal soft rays. Size and shape of pectoral fin could not be determined owing to left fin torn off in capture and right fin cut off for tissue sample. Pelvic fin below fourth spine of dorsal fin and behind origin of pectoral fin, its tip when depressed not extending to origin of anal fin. Anal fin with three strong spines, the first about half length of second, which is slightly longer than third spine; six soft rays forming narrow rounded tip to fin. Caudal fin weakly emarginate.

Scales all cycloid (excepting a hard, sharply spinulated suprascapular scale bone above the upper opening of the gill cover). Snout and dorsal surfaces of head naked anterior to a vertical passing through hind margin of preopercle. Interopercle finely scaled anteriorly and dorsally immediately below preopercular margin. Mandibular ramus with tiny thin scales covering most of posterior surfaces and extending forward onto lateral surfaces. Cheeks (viz, preopercle) finely scaled; hind (vertical) margin of preopercle finely serrated, but ventral margin smooth. Opercle and subopercle with large scales in two major rows bordered posteriorly with small scales. Chest and nape fully scaled. Eight scale rows along dorsal crest of nape before origin of first dorsal fin. Small scales at base of second dorsal fin (and sparsely on posterior base of spinous dorsal fin), and on bases of pectoral and caudal fins.

Anterior tip of premaxillary with cluster of small teeth and one enlarged canine more laterally placed; the cluster of teeth followed by a tapered band of small teeth. Dentary teeth consist of a cluster of small, short, conical teeth anteriorly that are rigid along outer margin but depressible inward of outer row. Posterior to these, a series of four larger canine-like teeth, with an outer smaller tooth row, these in turn followed posteriorly by a row of smaller teeth. Vomerine teeth small, in a broad short band. Presence of palatine teeth could not be adequately assessed for fear of damaging specimen; however, there appeared to be a row of small teeth along the bone.

Color (fresh)**:** (Fig. 8) Head with five or six small black spots behind eye, two in interorbital space, one on snout on median line, and diffuse ill-defined spots on sides of snout and head. Dorsal half of body and head darker than ventral half; nape and dorsum posteriorly to below third dorsal spine dark brown; a broad dark saddle below last three spines and first two soft rays of dorsal fin; a second dark saddle below 5th through 9th soft rays, followed by third saddle (partially merged with second) below last two soft rays and anterior one-third or so of caudal peduncle, a fourth saddle on posterior third of caudal peduncle ending sharply at base of caudal fin. Spinous dorsal fin irregularly brown with faint pale blotches, a bold black spot between posterior part of spinous dorsal and anteriormost end of soft dorsal fin; pectoral fin missing on both sides; pelvic fins pale to light yellow; anal fin dark brown overall; caudal fin mostly orangish to pink with darker upper and lower edges. Iris orange.

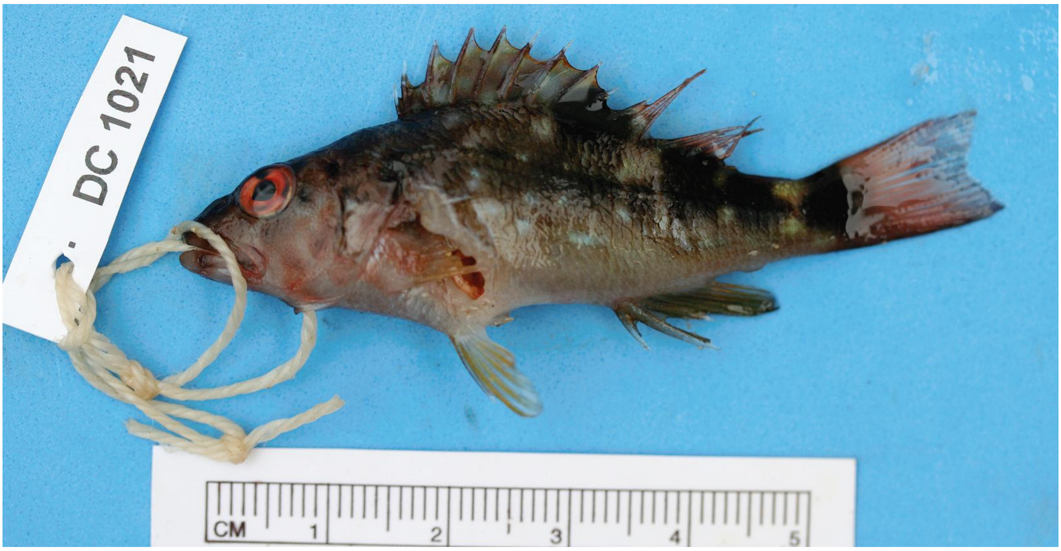

FIGURE 8. *Serranus drewesi* Iwamoto, new species. Holotype (CAS 234050 (53.5 mm SL) from submarine cave on Santana Islet, São Tomé Island. Photograph by David Catania.

Comparisons**:** *Serranus drewesi* is most similar in overall characters to *S. hepatus*, notably in having six anal fin rays and closely similar fin ray counts, somewhat similar body shape, and general color pattern, including a prominent black spot on the dorsal fin. That spot, however, is not ocellated as in *S. hepatus* and it merges with the broad saddle on the dorsum immediately below. The saddles on the body do not extend to the ventral body margin and do not sharply contrast with a generally pale body as in *S. hepatus*. The pelvic fin is overall yellowish (dusky in preserved specimen) in contrast to black in *S. hepatus* and the anal fin is uniformly dark brown without the pronounced black anterior and clear distal parts so notable in *S. hepatus*. Other differentiating features include: the absence in *S. drewesi* of narrow gold to orange stripes on the head (vs. present in *S. hepatus*); black spots on the head (lacking in *S. hepatus*), two opercular spines in *S. drewesi* (vs. three); snout longer than orbit (vs. about equal to); gill rakers on first arch 14 total (3+1+10) (vs. 19-23); long cirri on flap of anterior nostril 7 or 8 (vs. 1-3 stubby cirri); cycloid scales on body (vs. ctenoid scales); circumpeduncular scale rows 21 (vs. 23-26); scale rows below origin of dorsal fin 5 (vs. 6-8); interorbital space naked (vs. scaled); mandibular ramus finely scaled (vs. naked).

Serranus drewesi is readily differentiated from *S. scriba, S. cabrilla,* and *S. atricauda* by its fewer lateral-line scales and its distinctive color pattern. The combination of relatively low fin-ray counts of soft dorsal, pectoral, and anal fins, and the fewer gill rakers, the absence of ctenoid scales, as well as the color pattern, which includes a large black spot on the dorsal fin, distinguish the new species from the remaining eastern Atlantic species of the genus.

***Size*:** To at least 6.5 cm TL

DISTRIBUTION.— Known only from the holotype taken by mini-spear in a submarine cave in Santana Islet, Republic of São Tomé e Príncipe.

ETYMOLOGY.— Named in honor of Dr. Robert C. Drewes of the California Academy of Sciences, for his dedicated efforts in leading 12 separate scientific and educational expeditions to São Tomé e Príncipe to explore and document the diverse fauna and flora of that country and to inspire and educate the country's citizens as to the biological wealth and uniqueness of where they live.

REMARKS.— We describe this species with some reluctance owing to the absence of additional specimens and the small size of the only representative. We did not examine the internal organs, notably the gonads, to determine whether it is a juvenile or an adult. If the former, it is likely that the adult pigmentation pattern of this species differs substantially from the holotype. We also did not examine the myological, arthrological, and osteological characters used by Meisler (1987:80) defining the subgenera *Paracentropristis* and *Serranus* (e.g., levator arcus palatini muscle inserts on preopercle and dorsal origin of ethmomaxillary ligament medial on mesethmoid). We await the collection of additional specimens to expand on the description of this obscure little species.

TYPE SPECIMEN.— Holotype, CAS 234050 (53.5 mm SL); São Tomé e Príncipe, São Tomé Is.; Santana Islet (0°14′33.1″N, 6°45′36.1″W); collected by J.E. McCosker and J.-L. Testori in submarine cave at 62 ft [18.9 m] depth; 28 Jan. 2009; mini-hand spear.

***Serranus* (*Paracentropristis*) *hepatus* (Linnaeus, 1758)**

Figures 9–10

Labrus Hepatus Linnaeus, 1758:282 (Mediterranean).
Holocentrus siagonotus Delaroche, 1809:66, fig. 8 (Balearic Islands).
Serranus hepatus: Risso 1826:377. Dalgiç et al. 2013 (Black Sea off Rurkey), Apostolos 2014:142 (Black Sea, off Bulgaria)
Holocentrus adriaticus Nardo, 1827 (Adriatic).
Centropristis hepatus: Günther 1859:84 (Mediterranean).
Paracentropristis hepatus: Jordan and Evermann 1890:395. Fowler 1936:765, fig. 337.

DIAGNOSIS.— D X,11–13; P 13–15, usually 14; A III,6 or 7; gill rakers 6–7+14–15(19–23 total); pored lateral-line scales 44–52; circumpeduncular scales 23–26; scales below origin of first dorsal fin 6–8. Rim of anterior nostril elevated posteriorly forming a narrow flap bearing 1–4 fingerlike cirri at tip. Caudal fin emarginate, upper and lower lobes about equal. Interradial membranes of dorsal and anal fins scaled on basal one-half to one-third. Nape, interorbital, opercle (except outer margin), preopercle, interopercle, pectoral-fin base, and chest scaled. A prominent, ocellated black oval spot anteriorly on soft dorsal fin; pelvic fins black.

Description.— Body compressed, width across pectoral fin base about 2 in HL; greatest body depth about 2.8–3.0 in SL; head about 2.5–2.6 in SL. Dorsal profile from tip of snout to dorsal fin almost straight, thereafter broadly curved to caudal peduncle where it levels off; ventral profile moderately inclined from lower jaw to chest, leveling off on belly to origin of anal fin, then gently rising to caudal fin. Snout about equal in length to diameter of orbit; interorbital width

Figure 9. *Serranus hepatus*. From near Portimao, Algarve, Portugal. Photograph by Nuno Vasco Rodrigues.

Figure10. *Serranus hepatus* from Croatia, Adriatic Sea. Photo by Robert A. Patzner.

(fleshy) slightly less than orbit diameter; lower jaw projecting slightly beyond upper jaw; maxilla extending to below midorbit. Anterior nostril with raised rim, posteriorly becoming a narrow flap with 2–4 small fingerlike cirri or papillae at tip. Opercular spines three, the uppermost poorly developed and obscure, middle spine long and flat, the lowermost much smaller but evident. Preopercle margin serrated with flattened spines, those at angle largest.

Premaxillary teeth in narrow band, the outer series spaced and slightly enlarged with one or more large canines at anterior end where tooth band is broadest. Dentary teeth in band, with a spaced series of slightly enlarged outer teeth flanking small inner series in band, and largest teeth posteriorly in an irregular series. Vomerine teeth in broadly V-shaped band; a narrow band of small palatine teeth following close behind each end of vomerine band.

Small scales cover most of head (including interorbital space and fully scaled interopercle), body, and basal parts of all fins, but not snout, suborbital, jaws, gular and branchiostegal membranes, and free margin of preopercle, which are naked.

First 4–6 spines of dorsal fin graduated, the 6th through 8th spines usually longest, the spines following subequal; the soft rays about equal to or slightly higher than longest spines. Anal-fin rounded posteriorly; its spines much shorter than soft rays, the first spine somewhat more than half length of second and third spines, the anterior and middle soft rays longest. Pectoral fin broad-based, its origin about on same vertical as that of pelvic and dorsal fins; the pectoral and pelvic fins falling far short of anus. Caudal fin slightly emarginate.

Color (Figs. 9, 10) brownish-yellow or silvery with four or five prominent dark vertical bands; band below soft dorsal fin broadest and darkest, bifurcating dorsally to surround elongated black ocellus on soft dorsal fin, band ventrally entering basal half of anal fin. Band on nape often obscure; a small dark spot often present on caudal peduncle. Three or four narrow copper, gold, or brownish diagonal streaks on cheeks; the lowermost streak running from tip of snout to below orbit to lower corner of gill cover. Soft dorsal and caudal fins pale orange, peppered with small white spots. Pectoral fin clear. Pelvic fins black, sometimes with pale to white base and leading edge. Basal half of anal fin black, distal half dusky to clear.

***Size*:** To about 25 cm TL.

HABITAT AND DISTRIBUTION.— Over seagrass, sand, mud, and rocks from coast to about 100 m. Portugal to Senegal; also Mediterranean Sea and Black Sea.

REMARKS.— Meisler (1987:163) reported that the nasal flap is simple, but we found one to four fingerlike cirri on the nasal flap of our larger specimens from CAS 20741; the small specimens from USNM 198923 showed little development of cirri.

SPECIMENS EXAMINED (10 spec.).— **Mediterranean Sea**: CAS-SU 20741 (6, 53.8–88.8 mm SL); Italy; Naples; collector E.C. Starks. USNM 198923 (4, 35.4–38.0 mm SL), Lebanon, Antelias; coll. C. J. George, 10 July 1963.

***Serranus* (*Paracentropristis*) *heterurus* Cadenat, 1937**

Figures 11–12

Paracentropristis heterurus Cadenat, 1937:456–457, figs 13–14 (Guinea; 38-65 m). Cadenat and Marchal 1963:1274 (*S. sanctaehelenae* distinguished from *S. heterurus*).

Serranus heterurus: Heemstra and Anderson 2016:2411(in part; descr. and fig. of *S. inexpectatus* n.sp.; coast of Guinea to Congo; 25–30 m). Wirtz and Iwamoto 2016: figs 12–15 (comparison with *S. pulcher*; specimens from Senegal, Cape Verde Is., São Tomé I, and Guinea)

DIAGNOSIS.— D X,12; P 14–15 (rarely 17), usually 14; A III,7; gill rakers 6-8+15–17 (21–25 total); pored lateral-line scales 45–47; circumpeduncular scales 19–23; scales below origin of first dorsal fin 5–6. Caudal fin truncate, the upper lobe slightly pointed and produced, lower lobe rounded. Anterior nostril tubelike with high fringed posterior flap. Interradial membranes of dorsal and anal fins scaled on basal one-half to one-third. Nape, opercle, preopercle, pectoral-fin base and chest scaled. Ground color dark red to reddish-orange with seven white vertical bands on body alternating with broad red bands or blocks. A prominent white or blue crescent mark behind orbit in life (dark in preserved specimens); small blue spots ventrally on snout, suborbital and upper lip, and blue to white diagonal streaks on lower part of operculum.

Description.— Body relatively slender and compressed, width over pectoral bases about half of HL, greatest body depth 2.5–3.0 in SL, slightly less than HL, which is about 2.5–2.6 in SL. Dorsal and ventral profiles gently curved from tip of snout to caudal fin. Snout about equal in length to orbit diameter; both somewhat greater than interorbital width. Lower jaw projecting slightly beyond upper jaw; maxilla extending to below midorbit. Anterior nostril with raised rim, posteriorly rising to a high narrow flap with 2–4 long fingerlike papillae or slender cirri at distal tip; posterior nostril lacking raised rim. Opercular spines three, the uppermost poorly developed and obscure, middle spine longest, the lowermost smaller. Preopercle margin serrated with flattened spines, those at angle largest.

Premaxillary teeth in narrow band, the outer series spaced and slightly enlarged; one or more large canines at anterior end. Dentary with a spaced series of slightly enlarged outer teeth flanking band of much smaller teeth, the tooth series becoming larger posteriorly to near end of gape. Vomerine teeth in broad V-shaped band, followed on each arm by a narrow band of small palatine teeth.

Scales cover most of head, body, and basal parts of dorsal, anal, caudal, and pectoral fins, but absent on the following: snout; on dorsal surfaces of head to front of nape; over suborbital region to above hind margin of maxilla; on jaws; along narrow border behind orbits; on gular and branchiostegal membranes; on entire exposed surfaces of interopercle; and along outer margin of preopercle.

First four to six spines of dorsal fin graduated, the 5th to 6th spines longest, the spines following subequal; the soft rays slightly higher than longest spines, the 4th or 5th ray longest; a slight notch in fin profile. Anal fin relatively high, its posterior tip rounded; spines shorter than soft rays, the first spine more than half length of second and third spines, the second spine longer and stouter than the others; the anterior and middle soft rays longest. Pectoral fin broad-based, its origin about on same vertical as that of dorsal fin and slightly behind that of pelvic fin; the posterior tips of pectoral and pelvic fins fall short of anus. Caudal fin truncate to somewhat emarginate; dorsal lobe slightly pointed, ventral lobe rounded at tip.

***Color*:** In a live individual from the Cape Verde Islands (Fig. 11), ground color dark wine-red, five broad red bands across body from caudal peduncle to (and touching) base of pectoral fin, another over nape and onto opercle; forward of that a narrower band on preopercle; seven narrow white bands interspersed between red bands of head and body; behind posterior rim of orbit a prominent narrow blue to white crescent-shaped mark; small blue spots cover head and vertical fins. In a fish from Guinea (CAS 234558) (Fig. 12), ground color light reddish-orange, dorsum somewhat darker, snout darkest; five broad dark vertical bands on body, each extending almost entire depth of body, with the exception of the anterior two which fade into white of belly; dark bands alternate with six pale narrower bands, the last dark band narrowest and on caudal peduncle, followed by narrow pale band at base of caudal fin. Two white streaks on cheek from lower part of preopercle extending diagonally downward to interopercle; a light blue crescent mark along hind border of orbit; small blue spots on head and vertical fins. Soft rays of dorsal and anal fins distally dark with trace of blue and speckled with small yellow to gold spots; posterior margins of dorsal and anal fins blackish. Caudal fin with narrow yellowish bands; upper and lower margins yel-

FIGURE11. *Serranus heterurus.* From Tarrafal, Santiago, Cape Verde Islands. Photograph by Patrick Louisy.

FIGURE 12. *Serranus heterurus.* CAS 234558 (73.2 mm SL) from Guinea in 28–29 m, *R/V Dr. Fridtjof Nansen* station. Photograph by T. Iwamoto.

low; traces of reddish splotches near base of fin. Pectoral fin clear reddish-orange; pelvic fins blackish distally.

***Size*:** 10 cm TL.

HABITAT AND DISTRIBUTION.— On rocky and marl bottoms in 20–65 m. A single specimen from Guinea (CAS 234558) was found amongst a large catch of pen shells, Pinnidae. Senegal, Guinea-Bissau, Guinea, Sierra Leone, Ghana, Cape Verde Islands and São Tomé Island.

REMARKS AND COMPARISONS.— *Serranus heterurus* has been confused with *S. sanctaehelenae*, with which it has sometimes been synonymized (e.g., Robins and Starck 1961: 290; Smith 1981:5; 1990:706). *Serranus heterurus* can be readily distinguished from *S. sanctaehelenae* by its much smaller adult size (10 cm TL cf. 24 cm), and the following characters that are lacking in *S. sanctaehelenae*: color pattern (crescent-shaped marking behind orbit; blue spots below orbit; ground color reddish to orange); presence of cirri or fringes on posterior rim of nostril; dorsal lobe of caudal fin slightly produced. *Serranus heterurus* and the closely related *S. pulcher* are similar in most meristic and morphometric values, but differ notably in color pattern: *S. pulcher* is usually an overall dark grey on the upper half of head, the lower part reddish, then white on the underside, broken by a moustache-like marking from upper jaw that tapers medially, the markings on each side almost meeting at interopercles; the white chest is marked by a red streak originating at angle of operculum and ending at origin of pelvic fins; no black spot or margin in dorsal fin; no dark spots or whitish crescent marks on head; pelvic fins usually completely white. A common color variant in São Tomé has broad orange to reddish stripes on body, one dorsally from nape to dorsal margin of caudal peduncle, a midlateral stripe from eye to center of caudal fin base, a third from lower part of head to ventral margin of caudal peduncle; juveniles of this variant may have midlateral and lower stripes black. Comparison of *S. heterurus* and *S. inexpectatus* are given in the description of the latter species.

We found much variability in the color patterns, markings, and shape in this species that has led to much confusion as to what species we are dealing with. The original description and illustration of the species by Cadenat (1937) clearly distinguish most specimens from the Cape Verde Islands, Senegal, São Tomé I., Príncipe I., and Guinea.

DNA evidence provided by Benjamin Victor suggests that *S. inexpectatus* is most closely related to *S. pulcher* and together they form a clade that is sister to *S. heterurus.* Victor's DNA sequences for *S. heterurus* came from specimens collected in the Cape Verde Islands; those for *S. inexpectatus* from Angola, Sierra Leone, and Senegal. We have not had the opportunity to examine the voucher specimens.

SPECIMENS EXAMINED (12 spec.).— **Guinea:** CAS 234712 (64.8 mm SL); 9°24.8′N, 14°36.6′W; 47–53 m; *R/V Dr Fridtjof Nansen* [*DFN*] CCLME Survey 2012, sta. 7; 11 May 2012. CAS 234711 (80.8 mm SL); 9°46′N, 14°46.1′W; 34–33 m; *R/V DFN* CCLME Survey 2012, sta. 16; 12 May 2012. CAS 234558 (73.2 mm SL); 10°03.7′N, 15°28.5′W; 28–29 m; *R/V DFN* CCLME Survey 2012, sta. 27; 14 May 2012. CAS 234709 (46.6 mm SL); 10.152°N, 15.9284°W; 35 m; *R/V DFN* CCLME Survey 2012; 14 May 2012. **São Tomé e Príncipe:** CAS 231614 (58.2 mm SL); São Tomé Island; 0°04.35′N, 6°38.77′E; 56–60 m; *R/V DFN* Survey 2010-04-05, sta. 23; 15 May 2010. CAS 231627 (66.8 mm SL); São Tomé Island; 65–55 m; *R/V DFN* Survey 2010-04-05, sta. 32; 18 May 2010. **Cape Verde Islands:** USNM 405101 (88.3 mm SL); 15°45′12″N, 23°05′27″W; 73–61m; *R/V DFN* Cape Verde 2011 Exped, sta. 10, coll. K. Wieber, 10 June 2011. USNM 405105 (75 mm SL), between Santiago and Boa Vista islands; 15°40′06″N, 23°11′15″W; 77–79 m; *R/V DFN* Cape Verde 2011 Exped, sta. 12, 10 June 2011. USNM 405181 (69 mm SL); 16°34′36″N, 23°51′24″W; 31–45 m; Cape Verde 2011 Exped., *DFN* sta. 28, coll. K. Wieber, 14 June 2011. ZSM 44703 (78.3 mm SL), ZSM 43730 (39.4 mm SL), ZSM 43051 (36.0 mm SL); Kingfisher Bay at Terrafal on Santiago I.; 15.275522°N, 23.459545°W; 19 m; coll. P. Wirtz, Oct. 2015.

Serranus (*Paracentropristis*) *inexpectatus* Wirtz and Iwamoto, sp. nov.

Figures 13–15

Paracentropristis heterurus: Poll 1954:72–73, fig. 20 (in part, descr. and fig. of *S. inexpectatus*; nw of Mayumba, Gabon). Heemstra and Anderson 2016:2411 (in part, descr. and fig. from Poll 1954, of *S. inexpectatus*).

DIAGNOSIS.— D X,12; P 17; A III,7; gill rakers 5–7+10–11 (15–18 total); pseudobranchial filaments about 22; pored lateral-line scales 46; circumpeduncular scales 21; scales below origin of first dorsal fin 4, below first segmented dorsal ray 3–3.5. Caudal fin truncate, the upper lobe slightly pointed, lower lobe somewhat rounded. Dorsal, anal, and pectoral fins scaly near base. Anterior nostril tubelike, rim low anteriorly but rising to a high narrow flap posteriorly, with 4–6 long cirri at distal tip; posterior nostril a simple opening lacking a raised rim. Prominent black blotch distally between dorsal fin spines 1 and 4. Five broad bands on body and another over nape;

the band under 5th to 10th spines descends to belly well removed from pectoral-fin base and to front of anal fin; band below anterior rays of soft dorsal fin descends to middle of anal-fin base.

Description.— Body relatively slender, width over pectoral bases about half of HL, 18–20% SL, greatest body depth below fifth or sixth dorsal spine about 2.9–3.1 in SL and less than HL, which is about 2.6 in SL. Dorsal profile (excluding eye) rising in a relatively straight line to origin of dorsal fin, then leveling off to about fifth or sixth spine before descending in a gentle curve to base of caudal fin; ventral profile gently curved from lower jaw to caudal fin; orbit diameter about 4 into HL, longer than snout length, both substantially more than interorbital width. Lower jaw projecting slightly beyond upper jaw; maxilla extending to below posterior half of pupil. Anterior nostril tubular, the rim posteriorly elevated into a high narrow flap with 4–6 long slender cirri at distal tip; posterior nostril lacking raised rim. Opercular spines three, the uppermost small and obscure, middle spine longest. Preopercle margin serrated with flattened spines, those at angle largest; vertical portion of margin slightly inflected to form shallow lobe at angle.

Premaxillary teeth in narrow band, the outer series spaced and slightly enlarged; one or more large canines at anterior end. Dentary with a band of small teeth flanked by a series of slightly enlarged outer teeth that become larger posteriorly. Vomerine tooth band broadly V-shaped, teeth along posterior edge of bone slightly larger; each arm of vomerine teeth followed by narrow band of small palatine teeth.

First four spines of dorsal fin graduated, the middle 4th to 6th spines longest, the spines following subequal; the soft rays slightly higher than longest spines, the 3rd to 5th soft ray longest; a slight notch in fin profile. Anal fin relatively high, spines shorter than soft rays, the first spine more than half length of second and third spines, the second spine longer and stouter than the others. Pectoral fin broad-based, its origin about on same vertical as that of dorsal and pelvic fins; middle of fin (7th to 8th rays) longest, extending to base of first or second anal spine; pelvic fin falls short of anus. Caudal fin emarginate; dorsal lobe weakly pointed, ventral lobe somewhat rounded at tip.

Scales ctenoid, body fully covered; head naked over snout, interorbital, suborbital region, outer margin of preopercle and over subopercle. Small scales on interradial membranes of dorsal fin, mostly confined to basal one-fourth to one-half of soft rays, but a few on membrane between spines. Anal and caudal fins also with small scales at base, but on caudal fin, scales extending more distally. Scales on pectoral fin limited to immediate base of fin.

Pigmentation pattern (Figs. 13, 14) of preserved type specimens from Angolan and Gabon**:** Six or seven vertical bands on body from nape to base of caudal fin. Bands originate along dorsal outline of body and descend ventrally before fading on abdomen or near ventral outline; pigmentation of bands under dorsal fin extend onto base of dorsal fin rays. Anteriormost band faint, beginning over nape and extending posteriorly to below 3rd or 4th dorsal spine; ventrally, band descends onto opercle and subopercle. Second band below 5th to 10th spines descending to behind posterior half of pectoral fin, gradually fading over abdomen. That band, as in *S. pulcher,* does not abut against the pectoral-fin base. Third band below 1st to 6th soft dorsal rays, descending to ventral outline over anterior anal soft rays. Fourth band below last four or five soft dorsal rays and extending slightly onto caudal peduncle. A fifth band at middle of caudal peduncle, followed by a sixth band over end of peduncle and partly onto base of caudal fin. Angolan specimens have characteristic dark spots on snout and suborbital, and a faint dark crescent mark on hind border of orbit; tiny, irregular (in shape, size and distribution) black speckles on posterior one-half of interorbital space—these absent on Gabon specimen, which is faded. However, a small dark dot present on both sides of head just behind upper margin of orbit in all three specimens. Dorsal, anal and lower half of caudal fins dusky with faint diagonal streaks. Anal fin overall dark dusky but faintly whitish

FIGURE 13. *Serranus inexpectatus* Wirtz & Iwamoto, new species. (a) Holotype, ZSM 45041 (72.4 mm SL) from Angola, 35-36 m; (b) Paratype, ZSM 32516 (75.1 mm SL), same data as for holotype. Photographs by Peter Wirtz.

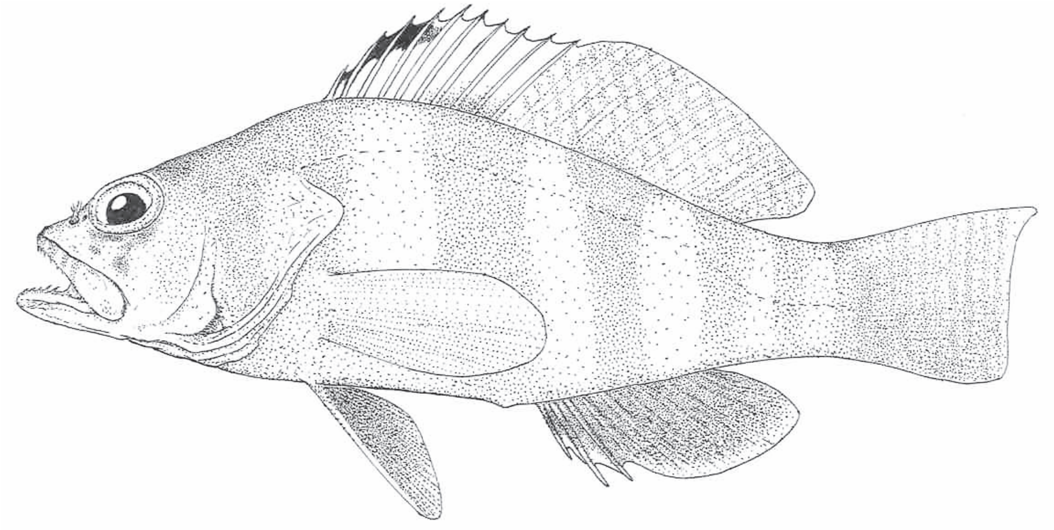

FIGURE14. *Serranus inexpectatus* Wirtz & Iwamoto, new species. Lateral view of holotype (ZSM 45041) showing markings on fins, body, and head. Markings have been slightly exaggerated.Drawing by Tomio Iwamoto.

FIGURE 15. *Serranus inexpectatus* Wirtz & Iwamoto, new species. A freshly collected specimen from Senegal. Photograph by Pascal Pépé Sjamajee Rommelaere.

FIGURE 16. *Serranus* sp. (possibly *inexpectatus*) living specimen collected in Sierra Leone. Photograph by Peter Wirtz.

FIGURE 17. *Serranus* sp. (possibly *inexpectatus*) preserved specimen collected in Sierra Leone. Photograph by Peter Wirtz.

along distal margin. Pelvic fins dark dusky except along leading ray, which is pale. Pectoral fin pale. Caudal fin dusky on ventral half, pale dorsally. Coloration in life from a photograph (Fig. 15) provided by Pascal Pépé Sjamajee Rommelaere of a specimen from Senegal shows the overall dark reddish to orange basic banding pattern (as described above for preserved specimens), but with the broad second band below the spinous dorsal fin splitting in two below the lateral line, and the band at caudal-fin base narrow and separated by a narrow pale band from the caudal rays. The black spot on the first three dorsal spines is quite prominent, as are the dusky pelvic and anal fins. Narrow reddish to orange streaks run along the dorsal and caudal fins and possibly the anal fin, although those on the anal are obscured by the overall dark-dusky fin coloration. Figures 16 and 17 show what are probably the new species taken off Sierra Leone. The coloration of fish from this country was quite different from those from Senegal. Rather than the overall pinkish to red of the Senegal specimens (Fig. 15), the Sierra Leone fish (Figs. 16 and 17) had a whitish to yellowish ground and dark reddish-brown bands and prominent red-orange blotches on top of head. A black mid-lateral stripe, faint anteriorly but dark posteriorly, extends from opercle to base of caudal fin, and merges with the black ventral surfaces of the lower caudal lobe.

***Size*:** To at least 92 mm TL.

HABITAT AND DISTRIBUTION.— Rocky bottoms in 25–36 m. So far known only from Senegal, Gabon, and Angola (and possibly Sierra Leone).

ETYMOLOGY.— From the Latin *inexpectatus*, meaning unexpected, surprising; in reference to

PW's surprising find of two specimens of an undescribed species in the collection of the Zoologische Staatssammlung, when looking at comparative material for the description of *Serranus pulcher*.

Remarks and comparisons.— PW initially examined the two Angolan specimens of this species and noted the slight shape differences between them and specimens of *S. heterurus*. However, almost all other morphological, meristic, and pigmentation characters appeared to fall within the range of variation we found in *S. heterurus,* lending doubt as to the distinctness of the two specimens. Poll's (1954: 72–73, fig. 20) description and accurate illustration of his single specimen from Gabon, which he called *Paracentropristis heterurus*, appeared to be exactly the same as the Angolan specimens, adding to the confusion. Ultimately, we are confident that Poll's specimen and our two Angolan specimens are the same undescribed species. Examination of many other specimens that agreed closely with Cadenat's (1937) original description and illustration of *S. heterurus* brought to light several key features that distinguish *S. inexpectatus* from *S. heterurus*. Most notable are the counts of pectoral-fin rays, gill rakers, and scale rows below the origin of dorsal fin (see Table 2). A one-ray difference in the count of pectoral-fin rays may seem rather insignificant, but the count of 17 rays (including the splintlike uppermost ray) in *S. inexpectatus* is consistent in the type specimens and not found in any of the 12 specimens of *S. heterurus* we examined. Meisler (1987: fig. 3) did record a count of 17 rays in 4 fins (of 22 fins total) in 11 specimens of *S. heterurus* he examined (see Table 2). We were not able to examine his material. Some proportional measurements (Table 3) appear to show differences between the two species, but with data from only three specimens of the new species, the significance of these differences must be substantiated with measurements of many more specimens. A distinct black blotch between the anteriormost three or four dorsal-fin spines in *S. inexpectatus* contrasts with the lack of such blotch in *S. heterurus* (although the distal margin of the spines may be blackish in some individuals of that species). In *S. inexpectatus* the broad band below the last four or five spines falls well behind the base of the pectoral fin and leaves a broad pale (or white) band or gap between the fin base and the dark band. In contrast, in *S. heterurus* the dark band below the middle of the spinous dorsal falls immediately behind the pelvic-fin base without a pale gap.

Type specimens.— **Angola.** Holotype: ZSM 45041 (75 mm SL) and paratype**:** ZSM 32516 (79 mm SL); 10°49′S, 13°43′E; 35–36 m; *R/V Dr Fridtjof Nansen* sta. 30147; 9 March 2003; coll. Reinhold Hanel. **Gabon.** Paratype: RBINS 9534 **(**73.8 mm TL), 30 miles NW of Mayumba, 3°11′S, 10°14′E; 25-30 m; Expédition Océanographique Belge sta. 164; collected with a small trawl over rocky bottom (catch included skates); 17 March 1940.

***Serranus* (*Paracentropristis*) *pulcher* Wirtz and Iwamoto, 2016**

Figures 18–21

Serranus sp. Kuiter, 2004:162 figs. A–D (São Tomé Comber; photographs taken by Peter Wirtz in São Tomé)
Serranus pulcher Wirtz and Iwamoto, 2016:192–199, figs. 1–15 (São Tomé e Príncipe; 1–30 m).

Diagnosis.— D X,12; P 15, rarely 14 or16; A III,7; gill rakers 6–9+12–14 (19–23 total); pored lateral-line scales 42–49; circumpeduncular scales 22–24; scales below origin of first dorsal fin 5–6. Caudal fin truncate, the upper lobe slightly produced, lower lobe rounded. Dorsal, anal, and pectoral fins scaly near base. Anterior nostril tubelike, rim low anteriorly but rising to a high narrow flap posteriorly, with 4–6 long cirri at distal tip; posterior nostril a simple opening lacking a raised rim. Seven or eight transverse bands on body; lips red with dark bands; a short moustache-like red streak behind end of maxillary, running across hind margin of dentary and almost meeting opposite streak at midventral line and enclosing ivory-white of mandibular rami; another red diagonal streak running from upper edge of maxillary, across lower edge of preopercle, across interopercle and branchiostegal rays, to base of pelvic fin, and enclosing white of preopercle, interopercle and chest.

DESCRIPTION.— Body relatively slender to moderately deep and compressed, width over pectoral bases about half of HL, greatest body depth about 2.7–3.2 in SL and less than HL, which is about 2.4–2.6 in SL. Dorsal and ventral profiles gently curved from tip of snout to caudal fin. Snout shorter in length than orbit diameter; both substantially more than interorbital width. Lower jaw projecting slightly beyond upper jaw; maxilla extending to below posterior half of pupil. Anterior nostril tubular, the rim posteriorly elevated into a high narrow flap with 4–6 long slender cirri at distal tip; posterior nostril lacking raised rim. Opercular spines three, the uppermost small and often obscure, middle spine longest. Preopercle margin serrated with flattened spines, those at angle largest.

Premaxillary teeth in narrow band, the outer series spaced and slightly enlarged; one or more large canines at anterior end. Dentary with a band of small teeth flanked by a series of slightly enlarged outer teeth that become larger posteriorly. Vomerine tooth band broadly V-shaped, each arm followed by narrow band of small palatine teeth. First four to five spines of dorsal fin graduated, the 3rd to 5th spines longest, the spines following subequal; the soft rays slightly higher than longest spines, the 3rd to 5th ray longest; a slight notch in fin profile. Anal fin relatively high, its posterior tip somewhat pointed; spines shorter than soft rays, the first spine more than half length of second and third spines, the second spine longer and stouter than the others. Pectoral fin broad-based, its origin about on same vertical as that of dorsal and pelvic fins; the tip of pectoral fin extends to, or almost to, anus, that of pelvic fin falls short of anus, both fins falling well short of anal-fin origin. Caudal fin truncate; dorsal lobe slightly pointed, ventral lobe rounded at tip.

Scales ctenoid, body fully covered; head naked over snout, interorbital, suborbital region, outer margin of preopercle and over subopercle. Small scales on interradial membranes of dorsal fin, mostly confined to basal one-fourth to one-half of soft rays, but a few on membrane between spines. Anal and caudal fins also with small scales at base, but on caudal fin, scales extending more distally. Scales on pectoral fin limited to immediate base of fin.

Color highly variable: in a fresh specimen from São Tomé Island (CAS 227751, 56.6 mm SL) dorsal aspects of head and body grayish brown to olive, this color extending down sides of head onto entire surface of opercle and most of preopercle but not interopercle and jaws; on body the ground color extends to mid-lateral line, below which the color becomes whitish to reddish and is dissected by seven or eight broad, red or brownish vertical bands that originate along dorsal outline of body and extend dorsally onto base of dorsal fin and ventrally to, or near, ventral outline. A faint brownish longitudinal stripe runs from upper lobe of opercle just above mid-lateral line to caudal fin base. Upper and lower lips deep red, but marked with dark bluish-gray bands and spots; lower lip with few faint bands or spots. A prominent red diagonal stripe from upper edge of maxillary, across interopercle, branchiostegal rays, and chest to base of pelvic fin. A short tapered moustache-like red streak behind end of maxilla, running across hind margin of dentary and almost meeting opposite streak at median-ventral line (see Fig. 18). Two other diffuse diagonal red streaks behind lower half of opercle extend onto pectoral-fin base. Branchiostegal rays, gular membrane, ramus of lower jaw, chest, and antero-ventral parts of belly white except where marked by red streaks. Soft dorsal and anal fins dark grey-brown with small orange spots that form narrow, broken, diagonal to horizontal lines on fins. Pectoral fin clear with orange tint. Pelvic fins dusky with small orange spots; caudal fin yellow on upper and lower lobes, membrane between rays clear with small orange spots that form vertical lines on tail.

In a photograph of a 35.3 mm SL specimen (CAS 227758) (Fig. 19) from Príncipe (Isla

FIGURE 18. *Serranus pulcher* from São Tomé Island showing color pattern on chin and throat. Photo by Peter Wirtz.

FIGURE19. *Serranus pulcher* A freshly collected specimen (paratype, CAS 227758, 36.3 mm SL) from Santana Islet, São Tomé. Photograph by David Catania.

Santana), brownish color of sides of head interrupted by four or five thin, horizontal to slightly diagonal, reddish to orange lines; orange spots scattered on top of head and on snout. Vertical bands on body with dark squarish blocks mid-laterally. Anal and soft dorsal fins dark; spinous dorsal paler with red spots at base where body bands meet fin; tips of spines red. Ivory-white of gular and branchiostegal membranes, interopercle, and chest bordered by prominent dark-red streaks. Pelvic fins overall clear to light dusky with brownish-yellow rays.

A fish from Príncipe (Fig. 20) shows a prominent, broad, brownish–red, broken midlateral stripe extending from midorbit to middle of caudal fin, bordered above and below by irregular

FIGURE 20. *Serranus pulcher* from Príncipe Island. Photograph by by Luiz Rocha.

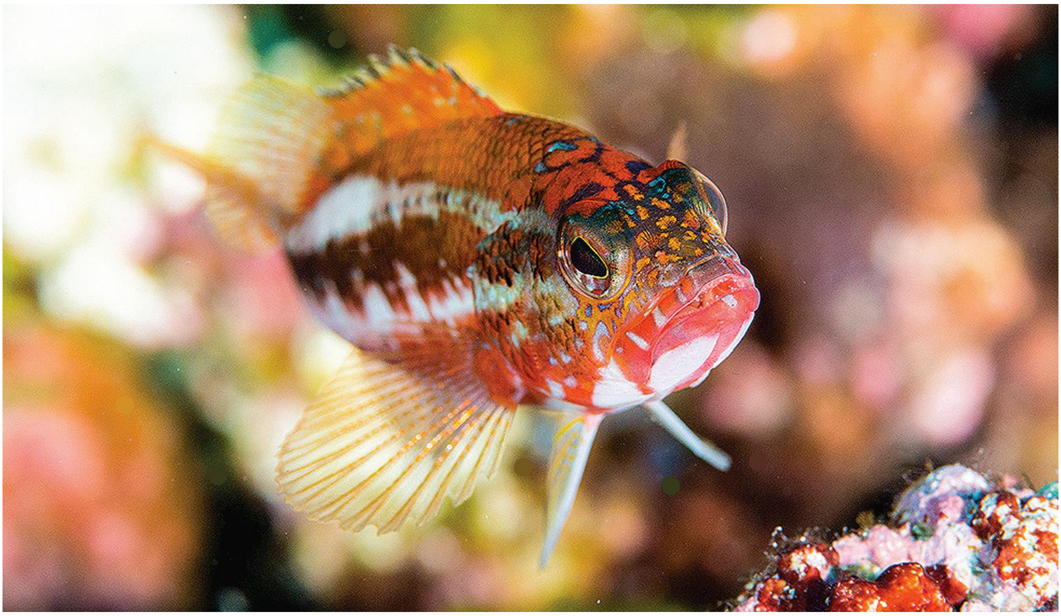

FIGURE 21. *Serranus pulcher*. A different-colored morph from Príncipe Island. Photograph by Luiz Rocha.

white stripes, the dorsum with broad brownish patches between white patches, and the ventral aspects of the body a solid dark red.

In a photograph (Fig. 21) of an individual from Príncipe, ground color orange with bold white stripes bordering a dark midlateral stripe that originates behind eye and extends to base of caudal fin; top of head, suborbital region, and snout dark gray with orange spots and vermiculations. In preserved specimens < 40 mm SL, midlateral stripe most prominent and other markings rather obscure. This color morph appears to predominate in Príncipe, where the species is quite common (Luiz Rocha, pers. comm. 2015).

***Size*:** To 9 cm TL.

HABITAT AND DISTRIBUTION.— Hard bottoms (rock, gravel, coral rubble, or marl) from about 1 m depth (juveniles) to at least 30 m. São Tomé e Príncipe, off Ghana and Gabon, and probably more widely along Gulf of Guinea mainland.

SPECIMENS EXAMINED (9 spec.).— **São Tomé e Príncipe:** CAS 227754 (4, 37.2–60.2 mm SL);

Príncipe Is., nw side of Bom Bom Is.; 1°41′44″N, 7°24′0.3″E; 48 ft [14.6 m]; collectors J.E. McCosker, D. Catania; 20 Jan. 2009. CAS 227753 (1, 58.5 mm SL); 1°41′09.3″N, 7°28′07.6″E; 40 ft [12.2 m]; collectors J.E. McCosker, D. Catania; 23 Jan. 2009. CAS 227751 (1, 56.6 mm SL); Kia Reef; 0°25′0.01″N, 6°48′E; 25–40 ft [7.6–12.2 m]; collectors J.E. McCosker, D. Catania, J-L. Testori; 11 Jan. 2009. CAS 227755 (1, 54.8 mm SL); Kia Reef; 0°21′37.1″N, 6°43′08.5″E; 45–72 ft [13.7–21.9 m]; collectors J.E. McCosker, D. Catania, J-L. Testori; 11 Jan. 2009. CAS 227756 (2, 59.3–60.4 mm SL); São Tomé Is., Batalleo; 0°22′05.7″N, 6°45′41.6″E; collectors J.E. McCosker, D. Catania, E. Milson; 13 Jan. 2009.

Serranus sanctaehelenae **Boulenger, 1895**

Figure 22

Centropristis brasiliensis (not of Brisout): Günther 1859:85. Melliss 1875:102.
Serranus sanctae-helenae Boulenger, 1895:289, pl. XI (St. Helena). Cadenat and Marchal 1963:1273-1275 (descr.; numerous specimens from 100 m depth)
Paracentropristis sanctae-helenae: Fowler 1936:766.
Serranus sanctaehelenae: Edwards and Glass 1987:637. Heemstra and Anderson 2016:2412.

Diagnosis.— D X,12; P 18; A III,7; gill rakers 20–21 total, 14 or 15 on lower limb; lateral-line scales 46–52; circumpeduncular scales 32–34; scales below origin of first dorsal fin 5. Anterior nostril a simple tube lacking cirri or flaps. Snout about equal to or less than orbit diameter; upper jaw extends to below midorbit. Body depth about 3.5–4.0 into SL; head about 2.5–2.7 into SL. Caudal fin emarginate. Six broad brown bands on body: one on nape, four below dorsal fin, one on caudal peduncle; color overall buff, paler below; fins faintly yellow, without prominent markings.

Description (partially adapted from Boulenger 1895:289 and Heemstra and Anderson 2016:2412).— Body compressed, width across pectoral fin bases about 2.1–2.3 in HL; depth about 3.1–4.0 times in SL; head about 2.6 in SL. Dorsal and ventral profiles gently curved; snout pointed and equal to or longer than diameter of orbit, which goes 3.3–3.8 times in HL; fleshy interorbital width 1.3–1.6 times into orbit diameter. Lower jaw slightly projecting beyond upper jaw; maxilla extending to below middle of orbit. Anterior nostril with low anterior rim and short flap-like posterior rim without fringes. Posterior nostril lacking rim. Opercular spines three, middle spine well developed, upper and lower spines rudimentary. Preopercular margins finely serrated.

A broad tapered band of small pointed premaxilla teeth, flanked by outer series of spaced slightly enlarged teeth; a few enlarged teeth at anterior end along inner edge of band. Dentary teeth in single series laterally and a cluster of teeth at anterior end. Vomerine teeth in a V-shaped band; palatine teeth in a single series.

Scales large, ctenoid and present on all of body and most of head, but absent on lower jaws, gular and branchiostegal membranes, snout, top of head, anterior half of suborbital region, and a narrow naked strip along outer margin of preopercle; opercle, subopercle, and interopercle scaly, the scales in six to eight series on cheek. Scales absent on fins except near base of pectoral and caudal fins.

Dorsal fin originating above base of pectoral fin; spines increasing in size to the 4th through 6th spines, which are slightly short of half length of head, and exceeding longest soft rays; a notch between spinous and soft portions of fin. Pectoral fin obtusely pointed, somewhat longer than pelvic fin, its length about 75% of HL. Second anal spine about equal to or slightly shorter but stronger than 3rd spine. Caudal fin feebly emarginate.

Color (based on photograph of fresh specimen from St. Helena in Fig. 22): Body light buff to pale greenish-yellow becoming whitish ventrally; six brown bands or vertical blotches, the first

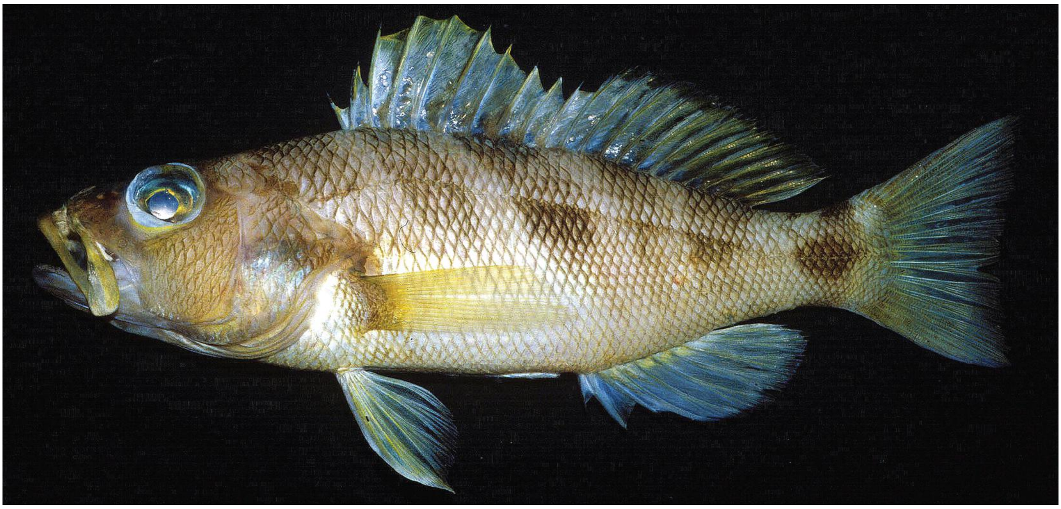

FIGURE 22. *Serranus sanctaehelenae* from Saint Helena Island. Photograph by Alasdair Edwards.

across nape extending to behind operculum, the second below first four or five spines, the third much darker and below last four or five spines; the fourth below third to fifth dorsal soft rays, the fifth below posterior half of soft dorsal, and the sixth on caudal peduncle forming a mid-lateral dark, oval, brown blotch; first four bands notably inclined. Head rather uniformly buff; operculum darker dorsally with a broad, diffuse, dark longitudinal stripe running from hind margin of preopercle to posterior edge of opercle; upper jaw light yellowish-brown. Fins mostly clear and faintly yellowish-green, but pectoral fin yellow with buff base.

Size: To about 24 cm TL.

HABITAT AND DISTRIBUTION.— Taken in about 100–110 m; endemic to St. Helena and Ascension Islands, where it is occasionally taken in the artisanal fisheries of those islands.

REMARKS.— Meisler (1987:144) was unable to assign this species to a subgenus owing to inadequate material.

SPECIMENS EXAMINED.— USNM 267902 (2, 178–180 mm SL); St. Helena Island; caught by fishermen on hook and line in deepwater (about 70–80 m); 9 July 1983; coll. Alasdair Edwards, field no. AE3-15.

***Serranus* (*Serranus*) *scriba* (Linnaeus, 1758)**

Figures 23– 24

Perca Scriba Linnaeus, 1758 (no locality)
Holocentrus argus Spinola, 1807.
Serranus scriba: Risso 1827:374.
Serranellus scriba: Jordan and Eigenmann 1890.
Paracentropristis scriba: Fowler 1936:766-768.

DIAGNOSIS.— D X,14–16; P 13–16; A III,7–8; gill rakers usually 7+12–14 (15–19 total); pored lateral-line scales 61–69 (60–73); circumpeduncular scales 36–41; scales below origin of first dorsal fin 6–9, below first branched ray 7–9. Scales on chest and cheek cycloid; all fins scaly along basal quarter or more. Caudal fin truncate or emarginate. Anterior nostril tube-like, with rim posteriorly developed into a tall fringed flap; posterior nostril with low, fringed anterior rim. Usually two (and often more) broad dark bands on body, a large white to bluish blotch on abdomen

FIGURE 23. *Serranus scriba* from El Cabrón dive site near Arinaga, Grande Canary Is., Canary Islands. Photograph by Rogelio Herrera.

FIGURE 24. *Serranus scriba* from Ibiza Island, western Mediterranean Sea. Photograph by Robert Patzner.

(in life); prominent reticulate to vermiform lines on head, and black horizontal stripe on snout, usually extending through eye onto dorsal margin of gill cover.

DESCRIPTION.— Body deep, about 33–37% SL; head low, profile of nape rises steeply into prominent arch; length of head 35–40% of SL; snout sharply pointed, 3.7–4.1 times in HL, orbit 5–6 times in HL, upper jaw slightly shorter than lower jaw. Dorsal profile of head rises in gentle curve, then abruptly ascends behind orbits to form a high, arched nape; profile peaking under middle of spinous dorsal before descending to caudal peduncle.

Premaxillary teeth canine-like in outer series, with narrow inner band of smaller teeth; dentary teeth in narrow band in front, band tapering to one row posteriorly; teeth at anterior and posterior ends largest. Teeth on vomer in narrow V-shaped band; those on palatines in one or two irregular series.

Margins of spinous dorsal fin moderately incised; spines increase gradually in height to peak at 4th or 5th spine, becoming shorter thereafter; in adults, no notch or indentation in fin outline where spinous and soft rays join, but juveniles have a slight indentation. Anal fin high, longest ray about equal to or higher than longest ray of dorsal fin; first anal spine 1.5–1.9 into second and third spines, which are more or less of equal length. Pectoral fin broad based, slightly pointed at tip; pectoral and pelvic fins fall short of anal-fin origin, a short streamer developed in pelvic fins between first and second rays in larger specimens.

Body fully covered with small ctenoid scales except on chest where scales cycloid; naked areas on head include snout, infraorbital bones, lower jaws, gular and branchiostegal membranes, and top of head posteriorly to beginning of nape; all opercular bones, pectoral-fin base, and chest scaled. Branchiostegal membrane and maxilla partially scaled in some specimens.

Color of live specimens (Figs. 23, 24)**:** Head with vermiform to reticulate pattern of light and dark lines; body with two to five broad to narrow brown to black bands that extend onto dorsal fin; the pattern with two broad dark bands appears to be typical in the eastern Atlantic and parts of the southwestern Mediterranean, the pattern with more, and often paired, narrower bands typical in the Mediterranean; the last band, caudal peduncle, and caudal fin often orange or yellow; tips of dorsal spines reddish-brown to scarlet; often a large bright-blue spot on sides of belly.

***Color of preserved specimen*:** Dark brownish overall, underside of head and chest paler, dorsal surfaces of head and all of nape dark, a horizontal dark stripe running from tip of upper jaw onto snout, through middle of eye onto dorsal margin of preopercle and opercle; a broad dark band below 5th to 9th dorsal spines; a darker band from base of 3rd dorsal soft ray to end of dorsal fin, narrowing ventrally and terminating at posterior half of anal-fin base onto anterior one-third or so of caudal peduncle. Head with irregular pale reticulate lines; upper jaw with blackish tip and series of four or more dark bands on maxillary; lower lip marked with dark bands; mandibular ramus with bold dark spots. Dorsal fin generally dark above the two broad body bands, the distal margin of soft dorsal fin with irregular speckling of small clear spots arranged in vertical to diagonal lines; anal fin with prominent sharp stripes distally; caudal fin relatively pale and lacking prominent markings; pectoral fin dusky with paler outer margins; pelvic fin blackish.

***Size*:** To 36 cm TL.

HABITAT AND DISTRIBUTION.— Over rocky bottoms from the shore to 150 m. Known from the Bay of Biscay to Senegal, including the Canary Islands but not the Azores, Madeira and the Cape Verde Islands; also in the Mediterranean and Black seas.

SPECIMENS EXAMINED (9 spec.).— **France:** CAS 238841 (ex. IU 7078) (3, 90.5–139 mm SL); Paris Market; collector D.S. Jordan. **Italy:** CAS 238072 (1, 131 mm SL); Mediterranean; Sicily; collector P. Doderlein, 1886. CAS-SU 20897 (2, 90.5–143.5 mm SL); Mediterranean; Naples; collector E.C. Starks. **Mauritania:** CAS 235486 (1, 161 mm SL); 18°36.93′N, 16°36.9′W; 30 m; *R/V Dr Fridtjof Nansen* CCLME Survey 2012, sta. 139, 3 June 2012. **Senegal:** CAS 15905 (2, 174–187 mm SL); Dakar; collector A.I. Good, 10 Nov. 1938.

FIGURE 25. *Chelidoperca africana.* A specimen 15 cm TL, taken off the Ivory Coast in 150 m depth. Photograph by Oddgeir Alvheim.

Key to species of *Serranus and Chelidoperca* in the eastern Atlantic

We have included the species *Chelidoperca africana* Cadenat, 1960 because it is frequently called *Serranus africanus* in the literature and is so treated by Smith (1990:704, CLOFETA], Williams and Carpenter (2015), and Heemstra and Anderson (2016).

1a) A III,6; D X,10–11, last two soft rays longest; pelvic-fin origin well in front of pectoral-fin base; body subcylindrical . . . . *Chelidoperca africana* Cadenat, 1960 (Fig. 25)
1b) A III,7–8 (rarely 6); D X, 12–16 (rarely 11); middle rays of soft dorsal fin longest; pelvic-fin origin below or only slightly in front of pectoral-fin base; body laterally compressed 2

2a) Lateral line scales 60–90 3
2b) Lateral line scales 40–52 5

3a) Nape distinctly arched; prominent vermiform or reticulate markings on head; lateral line scales 62–75; scales on cheeks and thoracic region cycloid; sensory canal system does not extend onto opercle; profile of dorsal fin not indented in adults . . . . *Serranus scriba* (Linnaeus, 1758)
3b) Nape not highly arched; no reticulate markings on head; lateral line scales 69–90; scales on cheeks and thoracic region ctenoid; sensory canal system extends onto opercle; profile of dorsal fin slightly indented 4

4a) D X,13–15 (rarely 12); A III,7–8, usually 7; circumpeduncular scales fewer than 47; caudal fin lacking black tips . . . . *Serranus cabrilla* (Linnaeus, 1758)
4b) D X,14–16; A III,7–8, usually 8; circumpeduncular scales 47 or more; caudal fin with black tips . . . . *Serranus atricauda* Günther, 1874

5a) A prominent black ocellated spot at beginning of soft dorsal fin; pelvic fins mostly black, but sometimes with white spine and pale basal section; interorbital space scaly. . . . .
. . . . *Serranus hepatus* (Linnaeus, 1766)
5b) No black ocellated spot on soft dorsal fin; pelvic fins pale to dark dusky; interorbital space naked 6

6a) A III,6; GR 14; scales all cycloid; a large black spot on dorsal fin between last 3 spines and first branched ray, the spot merging with black saddle on body; mandibular rami partially covered with small thin scales . . . . ***Serranus drewesi* Iwamoto, sp. nov.**
6b) A III,7 or 8; GR 19–26; scales ctenoid; no black spot on dorsal fin between last 3 spines and first branched ray; mandibular rami naked 7

7a) Scales present on interopercle; anterior nostril with a short elevated posterior flap that lacks cirri at distal tip . . . . *Serranus sanctaehelenae* Boulenger, 1895
7b) Interopercle naked; anterior nostril bearing cirri at tip of elevated posterior rim 8

8a) Caudal fin lunate to shallowly forked, often with a short streamer at tip of upper lobe; two blue stripes on head, one originating on snout and passing below orbit to end on lower margin of opercle, the other from posterior margin of orbit across gill cover and ending below middle opercular spine, last three anal-fin rays usually longer than those anteriorly . . . .
. . . . *Serranus accraensis* (Norman, 1931)

8b) Caudal fin truncate or emarginated, lacking streamer at tip of upper lobe; no blue stripes on sides of head, last three anal-fin rays usually shorter than those anteriorly 9

9a) Anteriormost body band below spinous dorsal fin descends onto belly immediately behind base of pectoral fin; a bright light blue or white crescent mark behind orbit. . . . . *Serranus heterurus* (Cadenat, 1937)

9b) Anteriormost body band below spinous dorsal fin descends onto belly well removed from base of pectoral fin and separated from same by a broad white (pale) band; no prominent white (pale) crescent mark behind orbit 10

10a) Anterior margin of spinous dorsal fin blackish or with a black blotch; pectoral-fin rays i16; gill rakers on first arch 15-18 . . . . ***Serranus inexpectatus* Wirtz and Iwamoto, sp. nov.**

10b) Distal margin of spinous dorsal fin lacking black margin or blotch; pectoral-fin rays i14-i15; gill rakers on first arch 19-22 . . . . *Serranus pulcher* Wirtz and Iwamoto, 2016

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Appendix

Table 1. List of species of *Serranus*

An asterisk (*) preceding the scientific name indicates that Meisler (1987:144) excludes the species from *Serranus*; despite their uncertain affinities, he states that "they appear to share more synapomorphies with *Diplectrum* than with *Serranus*." Subgeneric categories are those of Meisler

***Serranus* spp [14] from western Atlantic** (primarily from Heemstra, Anderson, and Lobel 2002:1308–1369. FAO Species Identification Guide for Fishery Purposes):

Serranus aliceae Carvalho-Filho & Ferreira. 2013. Size: 7 cm SL. Distribution: Brazil (between 8°N and 28°S).

Serranus (*Prionodes*) *annularis* (Günther, 1880). Size: 7 cm SL. Distribution: Georgia to Brazil, including Bermuda, nw Gulf of Mexico, and WI.

**Serranus atrobranchus* (Cuvier, 1829). Size: 9 cm SL. Distribution: Florida, n Gulf of Mexico to s Brazil (Santa Catarina).

Serranus (*Prionodes*) *baldwini* (Evermann & Marsh, 1900). Size: 6 cm SL. Distribution: s Florida, WI, Venezuela, Suriname, s Brazil (Santa Catarina; see Anderson et al. 2015).

Serranus (*Prionodes*) *chionaraia* Robins & Starck, 1961. Size: 5 cm SL. Distribution: Florida Keys, Honduras, Puerto Rico.

Serranus flaviventris (Cuvier, 1829). Size: 8 cm SL. Distribution: Venezuela, Brazil, Uruguay.

Serranus (*Mentiperca*) *luciopercanus* Poey, 1852. Size: 12 cm SL. Distribution: WI, Honduras.

**Serranus maytagi* Robins & Starck, 1961. Size: 9 cm SL. Distribution: central Caribbean.

**Serranus notospilus* Longley, 1935. Size: 8 cm SL. Distribution: Georgia, Florida Keys, Gulf of Mexico to Suriname.

**Serranus phoebe* Poey, 1851. Size: 15 cm SL. Distribution: Bermuda, North Carolina to Florida Keys, nw Gulf of Mexico, WI, Venezuela, Guyana, s Brazil (São Paulo).

Serranus subligarius (Cope, 1870). Size: 7 cm SL. Distribution: North Carolina to Texas.

Serranus (*Mentiperca*) *tabacarius* (Cuvier, 1829). Size: 17 cm SL. Distribution: Bermuda, Georgia, Florida, Gulf of Mexico, WI, Venezuela to Brazil.

Serranus (*Prionodes*) *tigrinus* (Bloch, 1790). Size: 10 cm SL. Distribution: Bermuda, s Florida, WI, Curaçao, Venezuela.

Serranus (*Mentiperca*) *tortugarum* Longley, 1935. Size: 8 cm SL. Distribution: s Florida, WI, Honduras, Panama, Venezuela.

***Serranus* spp [6] from eastern tropical Pacific** (from Robertson and Allen. 2015. Shorefishes of the Tropical Eastern Pacific: online information system. Version 2.0. Smithsonian Tropical Reserach Institute, Balboa, Panama. <*http://biogeodb.stri.si.edu/sfetp/*>):

**Serranus aequidens* Gilbert, 1890. (Deepwater serrano). Size: 24.5 cm. Distribution: s California to w Gulf of California; central Mexico to w Panama, Galapagos Islands, Cocos Island. Depth: 75–265 m.

**Serranus huascarii* Steindachner, 1900. (Peruvian serrano, Flag serrano). Size: 20 cm. Distribution: central Gulf of California to Chile. Depth: 80–200 m.

Serranus (*Prionodes*) *psittacinus* Valenciennes, 1846. (Bandred serrano, Banded serrano). Size: 18 cm. Distribution: central Baja to Gulf of California to Peru, the Galapagos. Depth: 2–60 m.

Serranus socorroensis Allen & Robertson, 1992. (Socorro serrano). Size: 8 cm. Distribution: Socorro Island (Revillagigedos Group). Depth: 5–20 m.

Serranus stilbostigma (Jordan & Bollmann, 1890). (Side-blotch serrano). Size: 14.5 cm. Distribution: Galapagos and Ecuador. Depth: 80–200 m.

Serranus tico Allen & Robertson, 1998. (Cocos serrano). Size: 8.5 cm. Distribution: Cocos and Malpelo Islands. Depth: 10–43 m.

***Serranus* spp. (10) from eastern Atlantic**:

Serranus (*Paracentropristis*) *accraensis* (Norman, 1931). Size: 20 cm TL. Distribution: Guinea Bissau to Angola, São Tomé Island

Serranus (*Serranus*) *atricauda* (Günther, 1874). Size: 35 cm TL. Distribution: Bay of Biscay to Guinea Bissau, including Azores, Madeira, Canary Islands., Cape Verde Islands, Mediterranean Sea.

Serranus (*Serranus*) *cabrilla* (Linnaeus, 1758). Size: 40 cm TL. Distribution: British Isles to South Africa (into Indian Ocean off Natal), including Azores, Madeira, Canary Islands, Príncipe Island, Mediterranean Sea and Black Sea; also Red Sea invasive.

Serranus (*Paracentropristis*) *drewesi* Iwamoto, new species. Size: 6.5 cm TL Distribution: São Tomé I.

Serranus (*Paracentropristis*) *hepatus* (Linnaeus, 1758). Size: 25 cm TL. Distribution: Portugal to Senegal; also Mediterranean Sea and Black Sea.

Serranus (*Paracentropristis*) *heterurus* Cadenat, 1937. Size: 14 cm TL. Distribution: Senegal to Angola, including São Tomé e Príncipe.

Serranus (*Paracentropristis*) *inexpectatus* Wirtz & Iwamoto, new species. Size: 9.6 cm TL. Distribution: Angola, Gabon, and Senegal (probably from Senegal south to Sierra Leone and east along African continental coast to Angola).

Serranus (*Paracentropristis*) *pulcher* Wirtz & Iwamoto, 2016. Size: 9 cm TL. Distribution: São Tomé and Príncipe; Ghana.

Serranus sanctaehelenae Boulenger, 1895. Size: 24 cm TL. Distribution: Saint Helena and Ascension islands

Serranus (*Serranus*) *scriba* (Linnaeus, 1758). Size: 36 cm TL. Distribution: Bay of Biscay south to Senegal, Canary Islands, Mediterranean Sea and Black Sea.

***Serranus* spp. (2) from the Indian Ocean**:

Serranus (*Serranus*) *knysnaensis* (Gilchrist, 1904). Distribution: South Africa (Cape of Good Hope to Natal).

Serranus (*Serranus*) *novemcinctus* Kner, 1865. Size: 32 cm. Distribution: Amsterdam and St. Paul Islands; Walters Shoals. Record from Cape of Good Hope probably erroneous (*fide* Heemstra and Randall 1986:537).

TABLE 2. Comparison of proportional measurements (in % head length) of *Serranus heterurus*, *S. pulcher,* and *S. inexpectatus*

Snout length

	20	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**n**	**mean**
heterurus	0	2	0	2	4	1	2	0	0	0	11	23.73
pulcher	0	2	2	4	0	3	0	1	0	1	13	23.70
inexpectatus	1	1	0	1	0	0	0	0	0	0	3	21.33

Orbit diameter

	22	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**n**	**mean**
heterurus	1	0	1	1	5	2	0	1	1	12	26.17
pulcher	1	0	2	2	1	1	3	0	2	12	26.42
inexpectatus	0	1	1	1	0	0	0	0	0	3	24.00

Interorbital width

	15	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**n**	**mean**
heterurus	0	0	1	1	1	2	3	1	2	11	20.45
pulcher	3	3	3	2	1	0	0	0	0	12	16.58
inexpectatus	1	2	0	0	0	0	0	0	0	3	15.67

Orbit-preopercle length

	33	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**n**	**mean**
heterurus	0	1	1	3	0	3	0	2	0	1	11	37.55
pulcher	0	1	4	1	2	2	0	2	0	0	12	36.67
inexpectatus	1	1	0	1	0	0	0	0	0	0	3	34.33

Length upper jaw

	43	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**n**	**mean**
heterurus	0	0	1	1	1	2	4	2	0	0	11	48.18
pulcher	0	0	1	1	3	1	1	3	0	1	11	48.27
inexpectatus	1	1	1	0	0	0	0	0	0	0	3	44.00

Length 2nd anal spine

	24	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**n**	**mean**
heterurus	1	1	1	2	2	1	0	2	0	0	0	0	0	10	27.60
pulcher	0	0	0	2	2	1	3	2	1	0	0	0	1	12	29.90
inexpectatus	0	0	0	0	0	0	1	0	2	0	0	0	0	3	31.33

TABLE 3. Comparison of fin-ray and gill-raker counts of *Serranus* spp. from the eastern Atlantic. (* denotes Meisler's [1987: figs. 3-4] counts included.)

Dorsal soft rays

	11	**12**	**13**	**14**	**15**	**n**	**mean**
accraensis		14*				14	12.00
atricauda				2	19*	21	14.90
cabrilla		1	11*	24*	1	37	13.68
drewesi	1					1	11.00
hepatus	1	19*				20	11.95
heterurus	1	20*				21	11.95
inexpectatus		3				3	12.00
pulcher		11				11	12.00
sanctaehelenae		5*				7	12.00
scriba				3*	26*	29	14.90

Anal rays

	6	**7**	**8**
accraensis		14*	
atricauda			19*
cabrilla	1	39*	1
drewesi	6		
hepatus	2	17*	
heterurus		20*	
inexpectatus		2	
pulcher		9	
sanctaehelenae		10*	
scriba		28*	1

Pectoral rays (uncertain if Meisler [1987: fig. 3] included small splintlike ray)

	13	**14**	**15**	**16**	**17**	**18**	**n**	**mean**
accraensis					25*	5*	30	17.17
atricauda			1	38*	3		42	15.81
cabrilla			41*	28*	2		41	15.45
drewesi		2					2	14.00
hepatus		2*	28*	2			32	16.00
heterurus			9*	23*	4*		36	15.86
inexpectatus					4		6	17.00
pulcher			2	21			23	15.91
sanctaehelenae					4*	6*	18	17.56
scriba	8	36*	1	11*	2		58	14.36

Table 3 (continued). Comparison of fin-ray and gill-raker of *Serranus* spp. from the eastern Atlantic.
(* denotes Meisler's [1987: figs. 3-4] counts included.)

	Gillraker counts (total)														
	14	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**n**	**mean**
accraensis					1*	1*	2*	1*						5	19.60
atricauda							7*	5*	5*	1*	1*			19	21.16
cabrilla					3*		1*	13*	2*	4*	1*	2*		26	21.42
drewesi	1													1	14.00
hepatus						1*		2*	5*	1*	1*			10	21.80
heterurus				1*			1	3*	3	2	5*	5	1*	21	23.00
inexpectatus		1			1									3	16.67
pulcher						1	5	2	2					10	20.50
sanctaehelenae							1*	2*	1*					4	21.00
scriba		1*		3*	8*	8*								20	18.10

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Louteridium (Acanthaceae: Acanthoideae: Ruellieae: Trichantherinae): Taxonomy, Phylogeny, Reproductive Biology, and Conservation

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***Louteridium* is treated as consisting of 11 species of mostly shrubs and trees that occur from northeastern Mexico to eastern Panama. Nine species occur in Mexico and six species are endemic there. *Louteridium* differs morphologically from other genera of the tribe Trichantherinae by its three-lobed calyx, gibbous-throated corolla, elongate anther thecae, and large pantoforate pollen. Characteristics of the calyx and pollen appear to be unique among Acanthaceae. RADsequencing yielded a highly resolved and for the most part strongly supported phylogenetic hypothesis for relationships among species of *Louteridium*, which itself is strongly supported as monophyletic. The three major clades recovered are treated as sections of the genus, with one of them newly described as *L.* section *Parcostamium*. Several approximate chromosome numbers are reported for the genus for the first time. Observations and experiments dealing with aspects of floral ecology and reproductive biology reveal that the primarily nocturnal flowers share morphological and chemical attributes commonly associated with pollination by bats. Both bats and hummingbirds have been observed visiting flowers, but pollinators have yet to be documented. Preliminary conservation assessments result in the inclusion of six species in a threatened category (five endangered and one critically endangered).**

KEYWORDS: Morphology, RADsequencing, pollen, chromosome numbers, phenology, chiropterophily, endemism

Louteridium S. Watson is a highly distinctive and geographically restricted Neotropical genus of Acanthaceae. Most of its species occur in Mexico, and most of them are rare and/or poorly collected. The large, primarily nocturnal flowers show several characteristics of adaptation to pollination by bats. Many new field collections combined with recent information on the ecology, reproductive biology, and phylogeny of species of *Louteridium* make the present monograph both a timely and comprehensive study of the genus. We also include information relevant to the conservation status of each species and offer preliminary conservation assessments for them.

Watson (1888) described *Louteridium* based on a collection from Guatemala. He placed the genus in tribe Ruellieae and noted three unusual features of the flower: a three-lobed calyx, an oblique and inflated corolla, and long-exserted stamens. A few years later, Baillon (1890) provided a detailed description of a new genus of Mexican plants, *Neolindenia*, which shared these (and other characteristics) with *Louteridium*, and the two genera are now considered to be congeneric. In his comprehensive and influential classification of Acanthaceae, Lindau (1895) treated the genus, known from a single species at the time, among the taxa with contorted corolla aestivation in its own tribe, Louteridieae, and noted its large, distinctive pollen and three calyx lobes. Bremekamp (1965:27) maintained tribe Louteridieae as distinct from Ruellieae on the basis of the "rather aberrant structure" of its pollen, and placed it in subfamily Ruellioideae. Recent classification schemes have treated the genus as Acanthoideae: Ruellieae: Ruelliinae (e.g., Scotland and Vollesen 2000), and most recently as Acanthoideae: Ruellieae: Trichantherinae (Tripp et al. 2013).

In a comprehensive taxonomic revision of *Louteridium*, Richardson (1972) recognized nine species: *L. brevicalyx*, *L. chartaceum*, *L. conzattii*, *L. costaricense*, *L. donnell-smithii*, *L. koelzii*, *L. mexicanum*, *L. parayi*, and *L. tamaulipense*. Since then, *Louteridium rzedowskianum* (Rzedowski 1973; Daniel 1984, 2017) and *L. dendropilosum* (Daniel 2017) have been described. Also, in an account of the genus in Chiapas, Daniel (1995) treated *L. conzattii* as conspecific with *L. mexicanum* and recognized *L. purpusii* as the correct name for the species treated as *L. mexicanum* by Richardson (1972). Richardson (1972) noted that species of *Louteridium* were poorly known and infrequently collected. Indeed, he was able to study only 71 collections (56 were cited) of the genus, six species were known to him by only one or two collections, and he made observations on a single species in nature.

In the present contribution, which builds on Richardson's (1972) important revision, 315 collections were studied, observations were made on six species in nature, and four species were studied in cultivation. As a result of our work, 11 species are herein recognized comprising a monophyletic *Louteridium*, which is sister to the other five genera of Trichantherinae (i.e., "core Trichantherinae"). Only one species is now known from fewer than four collections. Of the two sections of the genus recognized by Richardson (1972), one (section *Tetrandrium*) is maintained based on morphological, molecular, and habitat distinctions. Section *Louteridium* is revealed to correspond to two sections that are morphologically and ecologically similar, but which comprise separate clades within the genus.

Materials and Methods

Specimens and Living Plants.— More than 750 herbarium specimens representing 315 collections of all species of *Louteridium* were examined from 42 herbaria. In rare cases, when a digital image of a specimen was studied (via *http://plants.jstor.org/* or on the website of the herbarium cited), "image seen" is indicated. Four species were cultivated in pots at a greenhouse or on a lighted plant stand by a window in San Francisco from cuttings or seeds collected in nature. Plants of the following species (source locality and voucher number, which consists of the field collection number + *cv*) were subjected to various treatments and observations: *L. brevicalyx* (Mexico: Michoacán; *Daniel & Steinmann 11913cv*), *L. chartaceum* (Belize: Belize; *Daniel & Butterwick 5905cv*), *L. dendropilosum* (Mexico: Oaxaca; *Daniel et al. 11894cv*), and *L. mexicanum* (Mexico: Chiapas; *Breedlove & Daniel 70879cv*). Field observations on these, and two other species (i.e., *L. donnell-smithii*, *L. parayi*), were also conducted in native plant habitats. The observations, treatments, results, and interpretations are discussed under the appropriate sections below.

ddRAD Library Preparations.— To reconstruct phylogenetic relationships within *Louteridium*, facilitate understanding the evolution of morphological features among species, and test monophyly of Richardson's (1972) sections *Louteridium* and *Tetrandrium*, we generated and used ddRADseq data spanning multiple accessions of most species as follows. DNA was extracted from 30 samples of *Louteridium* representing all 11 species (Table 1). Of these, a minimum of two different collections were sampled for nine species; only one accession each of *L. brevicalyx* and *L. koelzii* were sequenced. Additionally, we extracted DNA from four species outside of *Louteridium* (one *Petalidium* plus three *Ruellia*; Table 1) but within tribe Ruellieae (Tripp et al.

TABLE 1. Information on accessions of *Louteridium* sampled for phylogenomic analysis, voucher information, number of ddRAD reads per sample, and year collected. Samples flagged as "Excluded" were removed prior to final analysis owing to insufficient read depth and/or quality. [1]This collection showed intermediacy in some characters with *L. donnell-smithii* and was treated as a potential hybrid by Daniel (1995).

Species	**Voucher**	No. Reads	Year Collected
L. brevicalyx	*Daniel & Steinmann 11913cv* (CAS)	2219763	2016
L. chartaceum	*Daniel 8294* (CAS)	2116162	1996
L. chartaceum-2	*Daniel & Butterwick 5905* (MO)	1922518	1989
L. costaricense	*Pennys 454* (CAS)	133385	1995
L. costaricense-2	*de Nevers et al. 6195* (CAS)	1374168	1985
L. costaricense-3	*Daniel s.n.* (CAS)	Excluded	1999
L. dendropilosum	*Zamudio 6352* (CAS)	3742842	1988
L. dendropilosum-2	*Daniel et al. 11894cv* (CAS)	2286789	2016
L. dendropilosum-3	*Daniel et al. 11784* (CAS)	1814475	2011
L. donnell-smithii	*Breedlove 41991* (DS)	3086698	1976
L. donnell-smithii-2	*Harper s.n.* (CAS)	3954078	2004
L. donnell-smithii-3	*Daniel et al. 11356* (CAS)	1302407	2010
L. donnell-smithii-4	*Daniel & Véliz 11255* (CAS)	4022387	2009
L. donnell-smithii-5	*Daniel & Véliz 11337* (CAS)	2695886	2010
L. donnell-smithii-6	*Evans 1001* (CAS)	3570992	1993
L. donnell-smithii-7	*Davidse & Brant 32089* (CAS)	Excluded	1987
L. koelzii	*McVaugh & Koelz 1797* (MICH)	2868788	1959
L. mexicanum	*Breedlove & Daniel 70879cv* (CAS)	5775753	1990
L. mexicanum-2	*Ventura 20989* (CAS)	494708	1984
L. mexicanum-3	*Hernández G. 1054* (CAS)	1035404	1985
L. mexicanum-4	[1]*Palacios E. 385* (CAS)	4219742	1988
L. parayi	*Vázquez et al. V-2566* (CAS)	479368	1982
L. parayi-2	*Breedlove & Daniel 70889* (CAS)	1838167	1988
L. parayi-3	*Daniel & Wendt 5804* (DUKE)	Excluded	1988
L. purpusii	*Breedlove & Smith 31613* (DS)	2725050	1973
L. purpusii-2	*Velásquez & López 1792* (CAS)	841011	2011
L. rzedowskianum	*Kruse 1380* (CAS)	5727927	1964
L. rzedowskianum-2	*Kruse 2701-b* (FCME)	1337471	1970
L. tamaulipense	*Hutchinson 60-889-1* (UC)	353608	1961
L. tamaulipense-2	*Valiente B. et al. 285* (MEXU)	1104339	1982
Petalidium halimoides × variabile	*Tripp & Dexter s.n.* (COLO)	118119	2017
Ruellia lasiostachya	*Tripp et al. 6778* (COLO)	6338722	2017
Ruellia puri	*Tripp et al. 5979* (COLO)	3238040	2017
Ruellia violacea	*Deward 244* (US)	2601741	1972

2013) to serve as outgroups, for a total of 34 accessions herein studied. DNA was extracted from field-dried materials using a CTAB protocol (Doyle and Doyle 1987). ddRAD libraries were prepared in-house using a custom protocol (Tripp et al. 2017) that was originally adapted from Parchman et al. 2012. Details are available in Tripp et al. (2017), and noted briefly here. Extracted DNA was first subjected to double digestion using *EcoR1* and *Mse1*. Illumina sequencing oligos that included custom designed, variable length barcodes affixed to the *EcoR1* cutsite were ligated onto digested fragments. Ten cycles of PCR were conducted to amplify restriction products, and this reaction was repeated once to ameliorate stochastic differences in PCR amplification. Agarose gels were used to assess DNA concentrations and sizes throughout the library prep protocol. Products of the two PCR reactions were pooled and then submitted to the University of Colorado's Biofrontiers Next-Gen Sequencing Facility for quality control and size selection. Fragments that ranged between 200 and 500 bp in length were size selected using BluePippin. Libraries from these 34 samples were pooled with libraries prepared by others and for other projects, and the final pooled libraries containing 96 multiplexed samples were submitted for 1x75 sequencing on an Illumina NextSeq v2 High Output Sequencer at Biofrontiers. All wet lab work was conducted in E. Tripp's molecular lab at the University of Colorado-Boulder.

BIOINFORMATICS AND PHYLOGENOMIC ANALYSES.— Raw data were downloaded and QC was assessed using FastQC (Andrews 2017), both before and after the trimming and discarding of overrepresented sequences. Illumina adapters were removed from reads using cutadapt v.1.4.2 (Martin 2011), implementing "-m 35" as the minimum required sequence length (35 bp) to retain a read. Reads were then demultiplexed using fastq-multx v.1.03, which is distributed as part of the ea-utils package (Aronesty 2011). We used the R function ggscatter() to visualize whether age of herbarium specimens impacted resulting numbers of raw reads, with the following argument: method = "pearson." Trimming of low quality bases, filtering, and *de novo* locus assembly steps were conducted using PyRAD v.3.0.66 (Eaton 2014). The following parameters were implemented: minimum coverage for retaining a cluster (Mindepth) = 5; maximum number of sites in a given locus with phread qualities < 20 (NQual) = 6; within-sample [step 3] and across-sample [step 6] clustering threshold (Wclust) = 0.85; and minimum number of samples required to retain a locus (MinCov) = 4. Additionally, Paralogous loci were excluded from further consideration by removing loci that contained more than two alleles with a given sample. A total of three samples was removed from the dataset and not considered further for analysis because of too few loci, resulting in a final taxon set consisting of 27 accessions of *Louteridium* plus four outgroups (Table 1). The resulting output phylip file was used in maximum likelihood (ML) phylogenetic inference implemented in RaxML v.8.2.9 (Stamatakis 2014). We used a GTR + G model of sequence evolution and conducted 100 rapid bootstrap replicates to assess branch support. A 50% majority rule consensus tree was calculated for each bootstrap tree, and branch support was summarized on the resultant most likely tree derived from the ML search. We considered branches to be supported if bootstrap values were $\geq$ 70%, with values nearer 70% taken to reflect low or weak support. *Petalidium* was used to root the final ML tree. All bioinformatic and phylogenomic work was conducted using the University of Colorado's SUMMIT supercomputer. The final RADseq phylogenomic dataset is available in GenBank under the Sequence Read Archive Study #SRP159283.

PHYLOGENY

INTERGENERIC RELATIONSHIPS.— *Louteridium* has traditionally been treated as a unigeneric tribe, Louterideae, of either Acanthoideae (e.g., Lindau 1895) or Ruellioideae (e.g., Bremekamp 1965). Molecular phylogenetic data for nearly all currently recognized genera of Ruellieae (Tripp

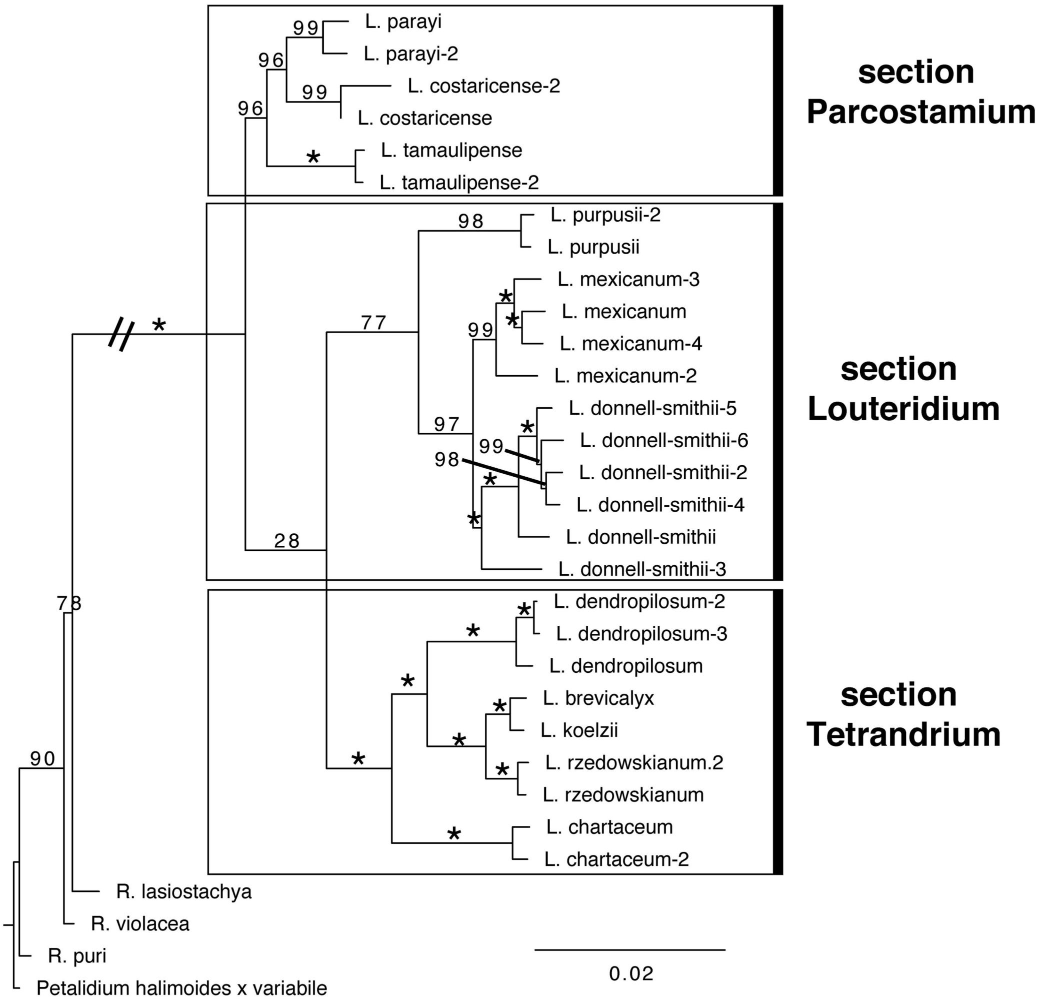


FIGURE 1. Most likely phylogenetic hypothesis for relationships among species of *Louteridium*, generated from ddRAD-seq loci analyzed under maximum likelihood (and implemented in RAxML). Our analyses yield strong support for a monophyletic *Louteridium* as well as support for three primary sections: *Louteridium*, *Parcostamium*, and *Tetrandrium*. Hash mark between outgroups and *Louteridium* indicate branch was shortened to reduced overall figure width for reproducibility. Asterisks [*] indicate 100% ML bootstrap support.

et al. 2013) reveal *Louteridium* to be sister to a morphologically similar and monophyletic lineage of five Neotropical genera treated as Trichanthereae (e.g., Lindau 1895; Bremekamp 1965; Daniel 1988, 2015): *Bravaisia* DC., *Sanchezia* Ruiz & Pav., *Suessenguthia* Merxm., *Trichanthera* Kunth, and *Trichosanchezia* Mildbr. Although the phylogenetic relationships and generic status of *Sanchezia*, *Suessenguthia*, and *Trichosanchezia* have yet to be fully resolved (cf. Schmidt-Lebuhn et al. 2005; Tripp et al. 2013), these five genera that together contain about 80 species, plus *Louteridium*, were proposed to form an expanded subtribe Trichantherinae of Ruellieae (Tripp et al. 2013).

Other than molecular characteristics, no synapomorphies are known for Trichantherinae. *Louteridium* shares a number of characteristics with remaining Trichantherinae, including arboreal habit and prop roots. These attributes are otherwise known, but relatively rare, among Acanthaceae. *Louteridium* differs conspicuously from other genera of Trichantherinae by its three-lobed calyx, gibbous-throated corolla, elongate thecae (6.5–17 mm long), and large (> 100 µm diam.) pantoforate (vs. loxodicolporate) pollen (Tripp et al. 2013; Daniel 1998, 2015). Each of these characters would thus appear to be synapomorphic for the genus. A possible additional synapomorphy for *Louteridium*, early abscission of unpollinated flowers at or near the base of the pedicel, is discussed below under Floral Ecology and Reproductive Biology.

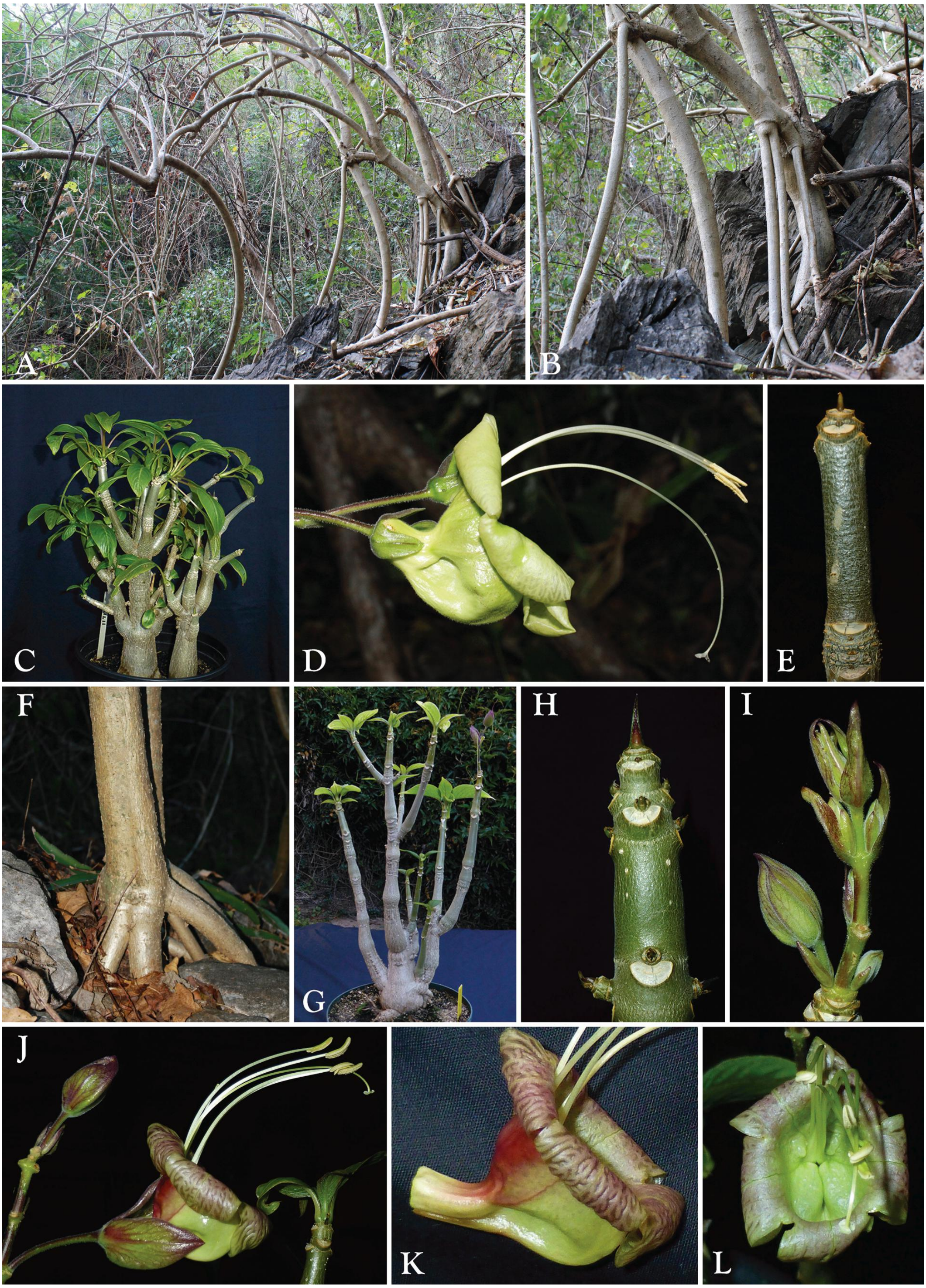
INTRAGENERIC PHYLOGENOMICS.— Our single lane of 96 multiplexed samples yielded a total of 493,303,821 reads (GC content = 49%) prior to trimming. Trimming removed Illumina single end adapter sequences as well as other overrepresented sequences, yielding a remaining set of 327,927,454 reads (sequence lengths between 35 and 92 bp; GC content = 40%). The total number of reads kept per sample (after filtering in PyRAD) is reported in Table 1. Of these, 51,072545 reads were "unmatched" during the demultiplex process and thus discarded from further consideration. We recovered no correlation between the year that herbarium material was collected and the total number of reads generated per sample (r=0.05; p=0.79; Table 1). The final phylip alignment file contained data from 31 samples and was 9,881,851 bp in length. Gaps and Ns constituted ~71% of this matrix.

The 27 accessions of *Louteridium* included in our final analysis were recovered as monophyletic with strong support (100% ML bootstrap [hereafter, BS]) based on outgroup sampling of two other genera (and four species) of Ruellieae (Fig. 1). Within *Louteridium*, our analyses recovered three major clades corresponding to three sections treated in the present study (Fig 1). *Louteridium* sections *Tetrandrium* and *Parcostamium* were strongly supported (100% and 96% BS, respectively), whereas section *Louteridium* was weakly supported (77% BS). Section *Parcostamium* was resolved as early diverging with respect to sections *Louteridium* and *Tetrandrium*, the latter two of which were resolved as sister lineages albeit without support. In all cases, multiple accessions representing a given species were recovered as reciprocally monophyletic to the exclusion of other species.

Thus, RADsequencing yielded a highly resolved and for the most part (only two branches unsupported) strongly supported phylogenetic hypothesis for relationships among species of *Louteridium*. Whereas section *Tetrandrium* reflects prior classification of four-staminate species comprising this group (Richardson 1972), our study recognizes two distinct, non-monophyletic lineages of two-staminate species (sections *Louteridium* and *Parcostamium)*. This departs from Richardson's (1972) classification in which he treated members of both of these clades as comprising the single section *Louteridium*.

Morphological characters indicative of or synapomorphic for each of the three clades varies. The presence of four stamens is a strong synapomorphy for species in section *Tetrandrium*, which are furthermore characterized by occurrence in dry forests, the presence of clustered leaves, and leaves that are seasonally deciduous. In contrast, species in both sections *Parcostamium* and *Louteridium*, which are characterized by flowers with two stamens, occur in moist to wet forests and have leaves that both persist throughout the year and are more or less evenly distributed along young stems. Morphological synapomorphies separating the latter two lineages are tenuous as currently understood; plants in section *Parcostamium* have somewhat succulent leaves, whereas plants

FIGURE 2. *Louteridium brevicalyx* (A-E) and *L. dendropilosum* (F-L). A. Habit and habitat. B. Trunk with adventitious roots on rocks. C. Six-year old cultivated plant with clusters of new leaves. D. Flower. E. Shoot apex showing clustered leaf scars. F. Base of trunk with adventitious roots on rocks. G. Six-year old cultivated plant with clusters of new leaves. H. Shoot apex showing clustered leaf scars. I Young inflorescence with bracts, bracteoles, and flower buds. J. Flower. K. Corolla showing invagination along base of throat. L. Internal view of corolla showing invaginations along base of throat. (A, B, *Daniel & Steinmann 11913*; C-E, *Daniel & Steinmann 11913cv*; F, *Daniel et al. 11784*; G-L, *Daniel et al. 11894cv*). Photos by T. Daniel.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in section *Louteridium* generally have membranaceous leaves. Geographically, species in section *Parcostamium* span the range of the genus, whereas species in section *Louteridium* occur only from southern Mexico to western Honduras. Although ancestral state reconstructions were not explicitly conducted on any character in this study owing to a relative paucity of terminals, it is plausible that plants that occurred in moist forests and plants having flowers with two stamens represent ancestral states in *Louteridium*, with later transitions to dry habitats and flowers with four stamens. Regarding stamen number, numerous other species in Trichantherinae (*sensu* Tripp et al. 2013) similarly have flowers with only two stamens. Regarding habitat, this hypothesis is congruent with data from other lineages of Acanthaceae, such as *Ruellia*, in which arid habitat lineages

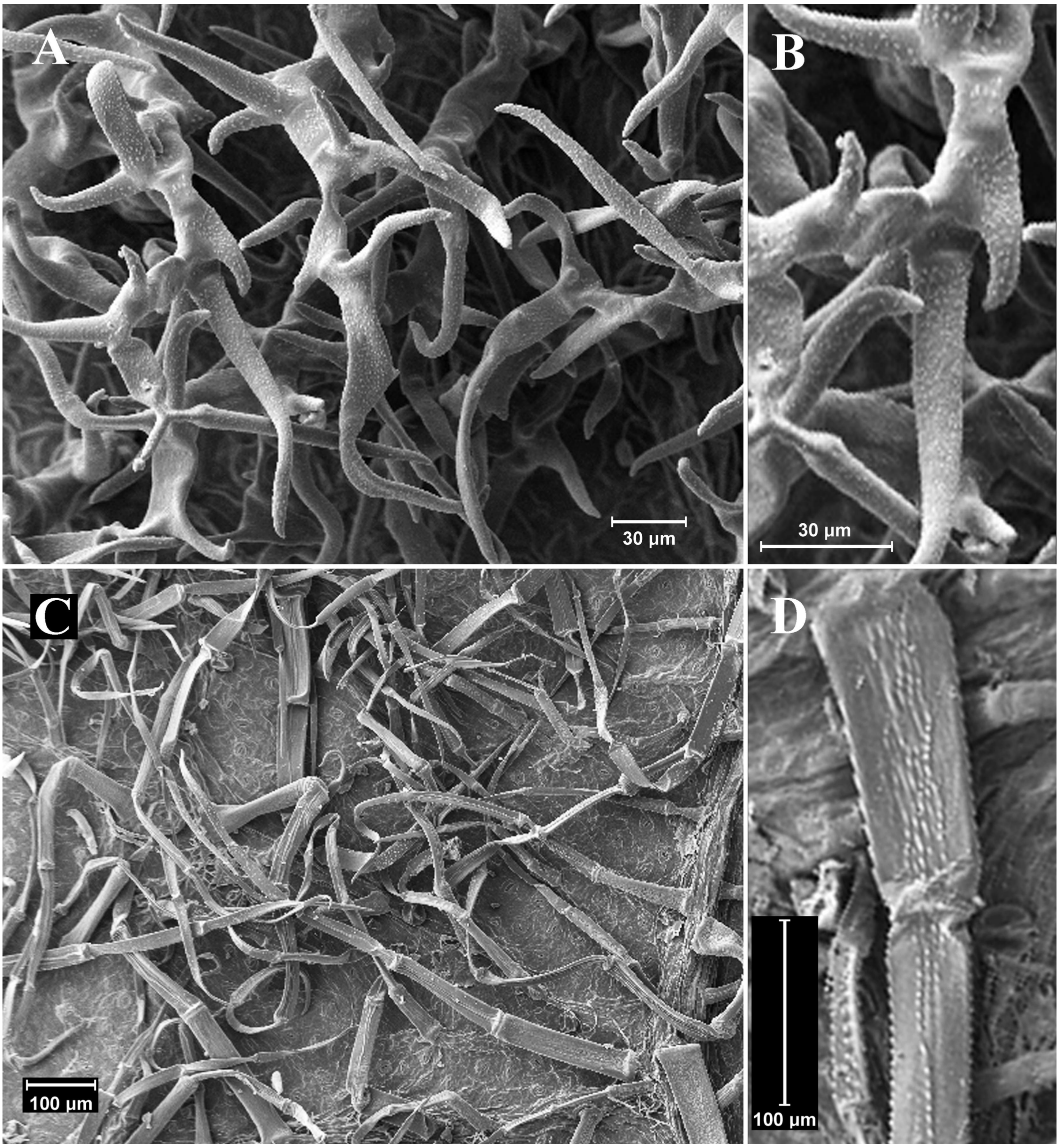


FIGURE 3. Trichomes (SEM) of *Louteridium* spp. A, B. *L. dendropilosum* (*Daniel et al. 11784*), with dendritic trichomes bearing scattered micropapillae. C, D. *L. donnell-smithii* (*Breedlove & Daniel 71197*), with unbranched trichomes bearing micropapillae mostly arranged in lines.

(e.g., dry forests, savannas) likely arose repeatedly from wet forest ancestors (Tripp 2007; Tripp and Tsai 2017). We cannot, however, rule out the likelihood that extinctions within *Louteridium*, whether representative of early diverging or later diverging lineages, may be confounding patterns of character evolution.

Within *Louteridium*, it is noteworthy that relationships resolved among species are compatible with morphological data and that RAD loci resolved all species as reciprocally monophyletic (Fig. 1). Our study thus adds to growing body of literature that documents the utility of RADsequencing within and across genera of flowering plants (e.g., Hipp et al. 2014; Tripp et al. 2017; Wang et al. 2017; Bateman et al. 2018). Within Acanthaceae, the *Petalidium* RAD dataset (Tripp et al. 2017) is the only one to have been published to date; however, the present study together with unpublished RAD datasets on two other genera (*Justicia*, Kiel et al., in prep.; *Ruellia*, Tripp et al., in prep.) brings the total number of lineages of Acanthaceae successfully sequenced using RAD loci to four.

MORPHOLOGY

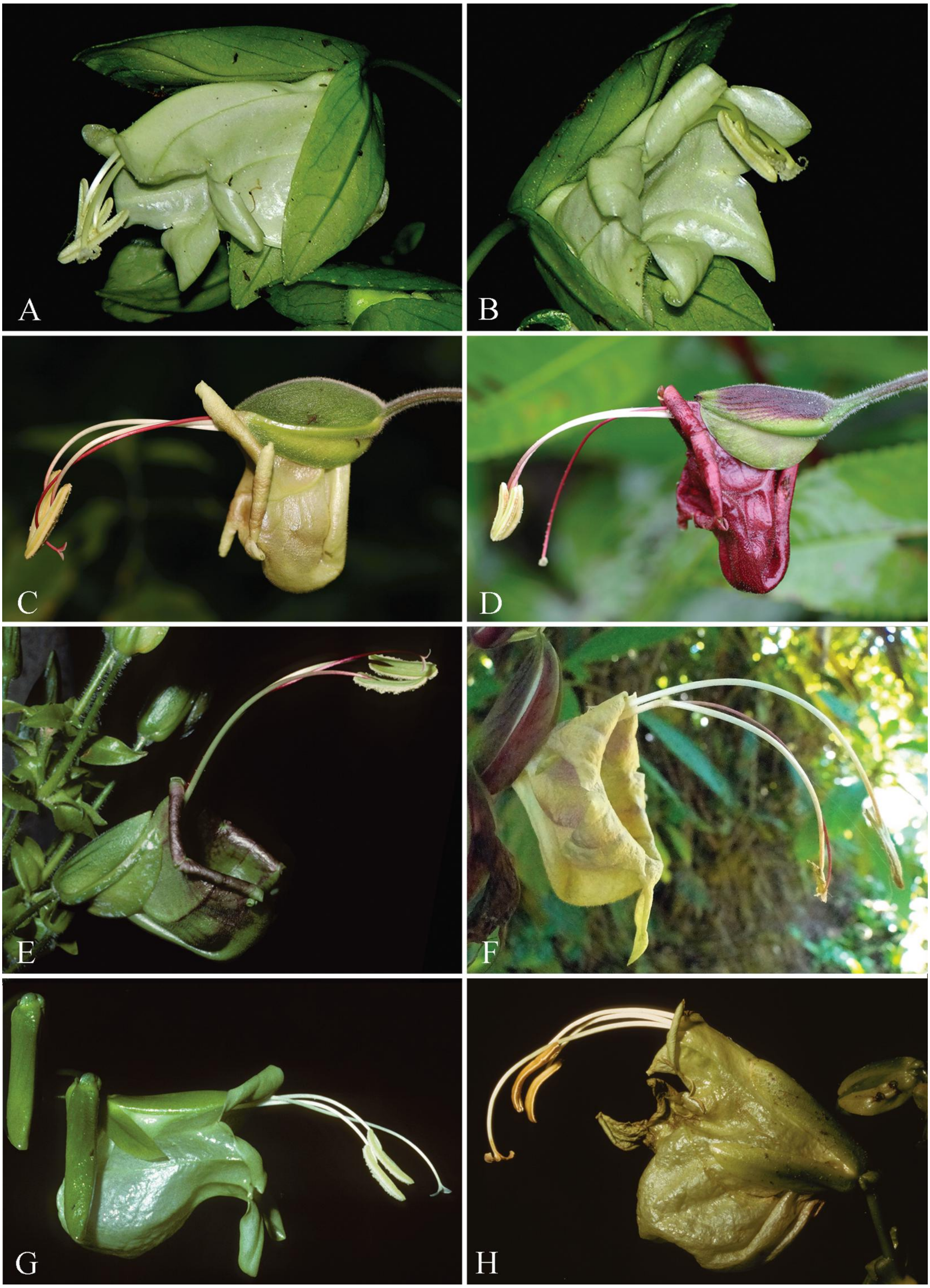
Because several species of *Louteridium* are not well known, discussions of some of the morphological variation in and unique or otherwise unusual characteristics of the genus are discussed below. Some morphological attributes for several species in the descriptions below are lacking due to their being absent or obscure on specimens, especially those that lack mature flowers or sufficient flowers for dissection.

HABIT.— Most species of *Louteridium* are reported to be trees (sometimes with multiple trunks, and sometimes described as “soft-wooded”) to 12 meters tall and with trunks to 25 centimeters in diameter, but several species can also occur as perennial herbs and shrubs. The three species of section *Parcostamium* are reported only as perennial herbs, shrubs, or small trees (to 3 meters tall). Both *L. costaricense* and *L. tamaulipense* are only known as perennial herbs or shrubs. *Louteridium parayi* is apparently only epipetric or epiphytic; and Richardson (1972:63) observed that *L. tamaulipense* was “sprawling and sending out adventitious roots on the rocks.” Based on limited substrate data, *L. costaricense* has been reported to be terrestrial. Species of section *Tetrandrium* are shrubs or usually trees. At least three of them are known to be mostly or entirely either epipetric or epiphytic. All three species of section *Louteridium* consist of both shrubs and trees and are terrestrial (or sometimes also epipetric in *L. donnell-smithii*).

Bark of the trees has been observed or reported as smooth to warty and gray to light yellowish brown or golden brown in color. Prop or adventitious roots have been observed in several species (e.g., *L. brevicalyx*, *L. dendropilosum*; Fig. 2A, B, F) and they have been noted by collectors on herbarium labels for others, including both trees and shrubs. Trees with multiple trunks and prop or adventitious roots are also known among several taxa of core Trichantherinae (e.g., *Bravaisia*, Daniel 1988; *Trichanthera*, Daniel 2015).

PUBESCENCE.— As in most other genera of Acanthaceae, a diversity of trichome types is encountered among species of *Louteridium*. Although some species are mostly (e.g., *L. parayi*) or entirely (i.e., *L. chartaceum*) lacking in elongate trichomes, either punctate glands (minute and sometimes flattened glands lacking a stalk), eglandular trichomes, or glandular trichomes (stalked glands) are apparently present on one or more surfaces in all species. Often mixtures of two or more of these trichome types co-occur. Dendritic (i.e., eglandular and branched one or more times) trichomes are known only in *L. dendropilosum* (Fig. 3A, B). Presence or absence of different types of trichomes on various parts of the plant, their relative lengths, and their shapes/stances are all useful in distinguishing among the eleven species treated here.

INFLORESCENCE.— The basic unit of the inflorescence in most Acanthaceae is a dichasium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that consists of a flower subtended by two homomorphic bracteoles. A bud is commonly present in one or both of the axils of the flower (or its pedicel) and each bracteole. From one or both of these buds, additional flowers, each subtended by two bracteoles, may develop into a multi-flowered dichasium. In *Louteridium*, the dichasia are sessile or pedunculate in the axil of a bract along a central axis, and the one to many flowers are usually borne on elongate pedicels from between the bracteoles. Herein, the inflorescences are referred to as racemes when the dichasia are sessile (but elongate pedicels are present), racemose thyrses when the dichasial peduncles are very short (e.g., 1 to 2 mm long), and thyrses when the dichasia are subtended by longer peduncles. Two or more of these configurations may occur in the same species, on the same plant, or in the same inflorescence (e.g., see below under *L. donnell-smithii*). As in other Acanthaceae, modifications on this pattern are evident among species of *Louteridium*. For example, the lateral dichasia are often expanded via sympodial growth and can appear like lateral inflorescence branches (e.g., *L. costaricense*, *L. tamaulipense*) or short-shoots (e.g., *L. chartaceum*, *L. purpusii*). These are sometimes mostly or exclusively basal (proximal) in the inflorescence (e.g., *L. tamaulipense*). The short-shoots are often somewhat tortuous or vary from linear (e.g., *L. chartaceum*) to fan-shaped (e.g., *L. purpusii*). In *L. mexicanum*, sympodial expansion of the dichasia can be either contracted or expanded and unbranched or branched.

Flower.— Flowers in *Louteridium* are nearly always borne on elongate pedicels that vary from (6 to) 20 to 105 mm in length. In spite of a gross similarity among flowers of *Louteridium*, there are numerous differences both within and among species. Some floral features are discussed in detail below because of either their taxonomic importance or their relevance to the reproductive biology of these plants.

The calyx of *Louteridium* consists of three lobes, which vary from distinct to basally fused for up to 3.5 mm. Because most (or all?) other Acanthaceae have five (rarely four) calyx lobes, the three-lobed calyx appears to be a morphological synapomorphy for the genus. Watson (1888:283) indicated that the two “upper sepals” were distinct and the lower three were united to the apex. He subsequently reversed this interpretation and indicated that the “three upper sepals” were united and the “lower two” remained distinct (Watson 1889:85). Bremekamp (1965) indicated that the calyx of *Louteridium* resulted from the fusion of the three anticous lobes. Whether by fusion or suppression of lobes, the developmental/evolutionary origin of the three-lobed calyx in *Louteridium* remains unknown. If by fusion, evidence from venation is equivocal. Both the posterior (= dorsal) lobe and the two lateral lobes have a single prominent midvein and sometimes one or more additional, more or less prominent, veins parallel to it on each side of the midvein (Fig. 4A, D, E). The lateral veins (and sometimes the midveins) can be inconspicuous or not evident in fresh or dried specimens. Although Watson’s correction in 1889 and Bremekamp’s agreement are possibly correct, none of the lateral veins is clearly identifiable as a “former midvein;” and total suppression of two lobes remains a possibility. Indeed, the presence of two additional and much-reduced calyx lobes on some flowers of *L. brevicalyx* (see under that species below) strongly suggests suppression. Developmental studies might ultimately determine the origin of the three-lobed calyx in *Louteridium*.

The three calyx lobes range in size from relatively small (i.e., 5 to 9 mm long in *L. rzedowskianum*) to subfoliose and larger (e.g., up to 65 mm long in *L. costaricense*). The lobes vary

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Figure 4 (left). Flowers of *Louteridium* spp. A, B. *L. costaricense* (*González 1977*), lateral and frontal views. C. *L. donnell-smithii* (*Daniel & Véliz 11337*), cream to green-yellow colored form. D. *L. donnell-smithii* (*Daniel et al. 11356*), chestnut to maroon colored form. E. *L. mexicanum* (*Breedlove & Daniel 70879cv*). F. *L. purpusii* (*Velásquez et al. 658*). G. *L. parayi* (*Daniel & Wendt 5805*) showing basally saccate dorsal calyx lobe on two buds at left. H. *L. parayi* (*Breedlove 24816*). Photos by D. Breedlove (H), T. Daniel (C-E, G), J. González (A-B), and L. Velásquez (F), used with permission.

from membranaceous to subsucculent in texture and from subhomomorphic to usually heteromorphic in form. When heteromorphic, the posterior lobe differs from the homomorphic lateral lobes either in size, shape, or configuration. The posterior lobe may be smaller or larger than the lateral lobes, and is often conduplicate (vs. planar in lateral lobes). In *L. parayi*, the posterior lobe is saccate or bears a two-parted flap of tissue at the basal portion of the abaxial surface that protrudes outward or downward from the abaxial surface for up to 2.5 mm (Fig. 4G); this feature is otherwise unknown in the genus and thus considered to be apomorphic for the species.

Corollas of *Louteridium* are primarily nocturnal, relatively large (35 to 72 mm in overall length), and mostly drably colored (white, yellow, greenish, dark chestnut to maroon, or brownish, and often with maroon discoloration or veins). Corollas that vary conspicuously in color were noted for some species (e.g., *L. donnell-smithii*, *L. mexicanum*). The tube consists of a relatively short (0.5 to 17 mm long) and subcylindric narrow proximal portion (from the base of the corolla usually to the point of insertion of the stamens) that abruptly and either symmetrically or asymmetrically expands distally into a large and obliquely bell-shaped (strongly saccate anteriorly) throat. The conspicuous throat extends from the point of insertion of the stamens distally to the base of the limb of the corolla. A linear or ± rectangular invagination of the corolla along each side of the anterior (= ventral) portion of the throat is evident in most species (Fig. 2D, K). It generally runs from near the junction of the narrow proximal portion of the corolla tube with the throat distally along the lateral sides of the throat toward the mouth of the corolla. It varies in size; for example, in *L. donnell-smithii* it is 17 to 25 mm long and 1 to 2 mm wide, whereas in *L. chartaceum*, it is 6 mm long and 4 mm wide. At least in *L. mexicanum*, the internal architecture of the corolla is complex. The lateral invaginations bear flanges (or ridges) along the posterior (upper) and anterior (lower) sides of their internal surfaces thereby forming a channel along most or all of the throat. Each lateral channel is closed proximally by the curved overlapping of the two flanking flanges, but these spread apart toward the distal end of the channel opening it on its inward-facing side near the mouth of the corolla. In addition to the lateral invaginations along the throat, there is also a ventral invagination with two internal flanges that form a nearly identical channel along the most or all of the anterior-most (basal) part of the throat. Collectively, the three invaginations/channels of the corolla, along with the filament curtain (see below), appear to form an extensive nectar chamber along the anterior portion of the saccate throat. Quantities of nectar examined in this species corroborate this conclusion (see Reproductive Biology). Lateral invaginations were noted to be present, but not as prominent internally in *L. donnell-smithii*; and although sometimes these were not clearly evident on the external surface in dried corollas of *L. parayi,* they are clearly evident on fresh corollas of that species (Fig. 4H). The subbilabiate limb consists of a bilobed upper lip and a trilobed lower lip; the lobes vary from spreading (i.e., ca. 90° from throat) to recurved to recoiled, thereby presenting a large (17 to 40 mm in diameter, measured from anterior to posterior points) and open mouth at the distal end of the throat. The lobes are shorter than the lips to which they pertain, and are either subequal or unequal in size (e.g., lobes of the upper lip are shorter and narrower than those of the lower lip in *L. parayi*). Internally, corollas are mostly glabrous except in the region of the tube at and proximal to the insertion of the staminal filaments. There, eglandular trichomes are present in most species (or absent, at least in *L. chartaceum*) and vary from sparse to dense.

The androecium consists of four stamens in section *Tetrandrium* and two stamens in sections *Louteridium* and *Parcostamium*. One or two usually short staminodes are commonly evident in the corolla tube as well. The epipetalous stamens are generally long-exserted from, and extend up to ca. five centimeters beyond, the posterior side of the corolla (Fig. 4). In *L. costaricense*, they tend to be exserted only about 1 to 1.5 cm beyond the upper lip of the corolla (Fig. 4A, B). The filaments generally curve upward then downward, forming an arc that is terminated by dangling anthers, free of obstructions. Filaments are inserted (i.e., emerge from) the internal surface of the corolla tube at or near (i.e., a few millimeters distal to) the junction of the narrow proximal portion and the throat. Anthers of all stamens in *Louteridium* bear two elongate (6.5 to 17 mm) thecae that are introrse, resulting in a nototribic flower.

In sections *Louteridium* and *Parcostamium*, there is a flat and somewhat quadrangular flange (ca. 4 to 5 mm long and wide) of tissue that is developed to a greater (e.g., *L. mexicanum*) or lesser (e.g., *L. donnell-smithii*) extent on both sides of the basal portion of each filament. On the posterior side of each filament the flange bears a short (0.5 to 3 mm long) triangular to subulate staminode; thus, the two staminodes are nearest to each other and between the filaments on the posterior side of the corolla tube. The adjacent flanges bearing staminodes from each filament do not fuse with one another. One or more staminode-like appendages are sometimes present on the distal portion of the flange on the opposite (anterior) side of the filament, but no veins go to this region. Flanges of both filaments (usually on the anterior side of each filament) taper as they extend 4 to 6 mm toward the base of the narrow proximal portion of the corolla tube. Collectively the flanges from the base of the filaments form a barrier or a portion of the “filament curtain” sensu Manktelow (2000) that creates a nectar chamber in which the ovary, proximal portion of the style, and nectar disk occur. Because the curtain may be oriented obliquely, the chamber does not always occupy the entire narrow proximal portion of the corolla tube. In *L. parayi* of section *Parcostamium*, the narrow proximal portion of the corolla tube is greatly reduced in length. In this species, there is a very pubescent flange along the base of the equally pubescent basal portion of each filament. Based on the position of staminodes in sections *Louteridium* and *Parcostamium*, the fertile pair of stamens in this section corresponds to the anterior pair of androecial elements.

In section *Tetrandrium* the four filaments are arranged pairwise in two different configurations. The anterior pair of filaments is inserted a few millimeters proximal to the posterior pair. Thus, although the stamens are usually equal in length, during anthesis the anthers of the latter pair are presented several millimeters beyond (i.e., in front of) those of the former pair. Each of the anterior filaments is connate with the adjacent posterior filament, such that each connate pair consist of two stamens inserted at different heights in the corolla tube. These pairs are connate at their bases for varying distances (e.g., 2 to 4 mm in *L. chartaceum* and 10 mm in *L. brevicalyx*) by a pubescent (or sometimes glabrous in *L. dendropilosum*) flange of tissue from the filaments. Together the filament flanges and the lateral invaginations of the anterior portion of the corolla throat noted above form a barrier to the nectar chamber similar to that described above for plants with two stamens. In *L. brevicalyx*, the nectar chamber appears to occupy the entire narrow proximal portion of the corolla tube. In species of section *Tetrandrium*, a narrow, pubescent, flange-like extension from the non-connate side of each of the proximally inserted filaments tapers 4 to 6 mm down the narrow proximal portion of the corolla tube. There is no fusion between the two pairs of connate stamens, thus potentially rendering the nectar chamber accessible by probing floral visitors. A single staminode, when present or evident, in section *Tetrandrium* is borne on the inner surface of the corolla tube in posterior-most position, between the two connate pairs of stamens in the vicinity of the zone of connation.

The types of filament curtains occurring among Acanthaceae, and a description of that in *L. mexicanum*, were provided by Manktelow (2000). In what is presumed to be a teretological androecium in a dissected flower of *L. mexicanum* (section *Louteridium*; *Breedlove & Daniel 78879cv*), a third fertile stamen appears to be borne in anterior-most position, and emerges at or very near the base of the corolla (ca. 13 mm proximal to the emergence of the remainder of the androecium).

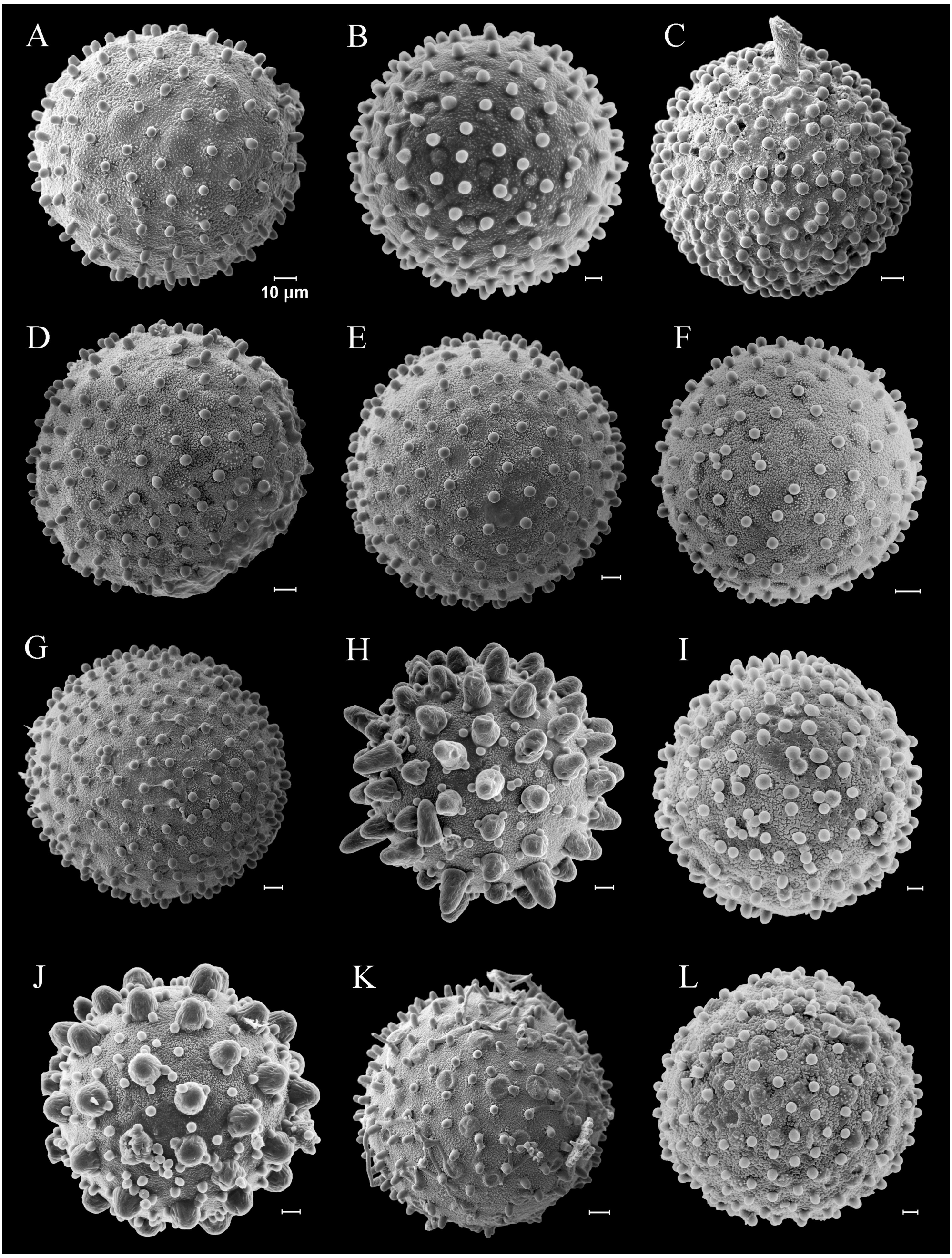


FIGURE 5. Pollen of *Louteridium* (except for *L. koelzii*, which was unavailable). A. *L. brevicalyx* (*Daniel & Steinmann 11913*). B. *L. chartaceum* (*Daniel & Butterwick 5905*). C. *L. costaricense* (*van der Werff 7019*). D. *L. dendropilosum* (*Daniel et al. 11784*). E. *L. donnell-smithii* (*Daniel & Véliz 11337*). F. *L. mexicanum* (*Breedlove & Thorne 30786*). G. *L. parayi* (*Daniel & Wendt 5805*). H. *L. parayi* (*Breedlove & Daniel 70889*) with intine protruding from apertures (revealing their number). I. *L. purpusii* (*Breedlove & Smith 31613*). J. *L. purpusii* (*Breedlove & Smith 31613*), with intine protruding from apertures (revealing their number). K. *L. rzedowskianum* (*Kruse 1380*). L. *L. tamaulipense* (*Hutchinson s.n.*). All scales = 10 µm.

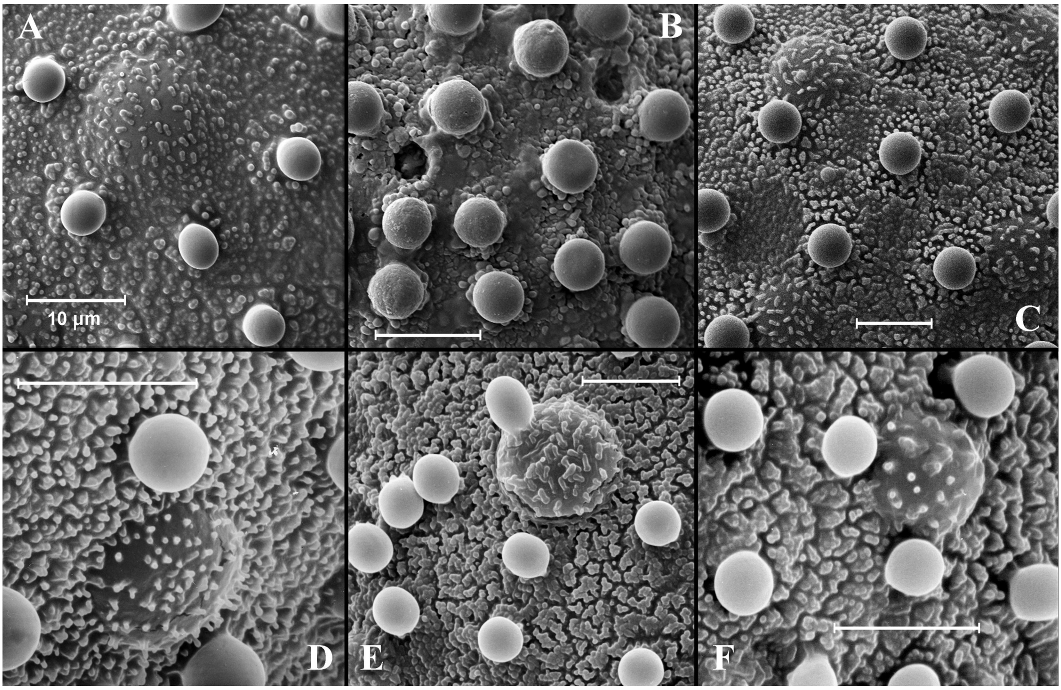


FIGURE 6. Pollen exine sculpturing of *Louteridium* spp. A. *L. brevicalyx* (*Daniel & Steinmann 11913*). B. *L. costaricense* (*van der Werff 7019*). C. *L. donnell-smithii* (*Daniel & Véliz 11337*). D. *L. mexicanum* (*Breedlove & Thorne 30786*). E. *L. purpusii* (*Breedlove & Smith 31613*). F. *L. tamaulipense* (*Hutchinson s.n.*). All scales = 10 µm.

The gynoecium consists of an oblong to subrectangular ovary that sits on or is partially embedded in a prominent nectar disk; a long-exserted style (less exserted in *L. costaricense*), which like the stamens is exserted from the posterior side of the mouth of the throat; and an equally to unequally bilobed stigma that is positioned near or exserted up to ca. 1.5 cm beyond (i.e., in front of) the anthers and either at about the same level or up to 1 cm or more above or below them. The ovary is glabrous or pubescent with trichomes like those of the capsule. The nectar disk is annular to ± cupulate, fleshy, up to 7 mm in diameter (when fresh), and 1.5 to 3 mm high.

POLLEN.— Pollen of all species of *Louteridium* except for *L. koelzii* (unavailable) was studied with scanning electron microscopy as described by Daniel (1998). Pollen of the ten species examined is remarkably uniform (Appendix 1 and Figs. 5, 6), and can be described as follows: spherical to subspheroidal (because polar and equatorial axes could not be determined in individual grains, a P:E ratio could not be determined; however, measuring the longest and shortest diameters gave ratios of 0.93 to 1.08), very large (106 to 143 µm in diameter; n = 29, mean = 122, SD = 10.88), and pantoforate; apertures more than 50, circular, 5 to 18 µm in diameter, and with surfaces usually ornamented like those of the interapertural exine; and interapertural exine with sculpturing elements of two non-overlapping sizes: the larger elements consist of gemmae (widest above base) to baculae (widest at base and not tapering apically) 3.0 to 6.3 µm in diameter and 1.7 to 7.0 µm high, the smaller sculptural elements are sparse to dense (sometimes jigsaw-like and nearly forming a reticulum) and vary from gemmae to pilae to baculae to echinae or are irregularly shaped verrucae to rugulae with the longest axis 0.1 to 2.5 µm. These smaller sculptural elements (and occasionally also a few of the larger elements as well) cover the apertures (Fig. 6), often rendering apertures visible in unacetolyzed grains only when the apertural surface and intine begin to bulge or protrude (e.g., Fig. 5H, J). Other studies of *Louteridium* pollen have noted the following ranges of diameters: 125 to 230 µm (nine species; Richardson 1972), 140 µm (*L. donnell-smithii*; Raj 1961), 187 to 206 µm (*L. parayi*; Palacios Chávez 1975), and 120 to 130 µm (*L. donnell-smithii*; Scotland 1993).

Pollen of *Louteridium* differs from all other genera of Acanthaceae (including Trichantherinae). Pollen of core Trichantherinae has been described as "loxodicolporate" (Daniel 1988, 1998, 2015) and as "rotationally symmetric" by Vasanthy and Pocock (1986); all five genera in this latter clade have pollen globose-oblong to globose-elongate, 2-colporate, polypseudocolpate, and with sculptural features of one face oriented 90° out of phase with those of the opposite face (e.g., Daniel 1998, fig. 3; Tripp et al. 2013, fig. 14; Daniel 2015, fig. 1). This type of pollen appears to be unique among extant pollen-bearing plants (although also known in the fossil record; see discussions in Tripp and McDade 2014 and Daniel 2015). Among other Ruellieae, pollen of *Louteridium* is similar to that of *Brunoniella* Bremek. and *Acanthopale* C.B. Clarke (e.g., Tripp et al. 2013, fig. 14); all three genera are pantoforate with ± similar interapertural ornamentation. Pollen of *Louteridium* appears to be unique among Acanthaceae by the combination of these sculptural elements combined with the exceptionally large size of the grains and high number of apertures. Pollen of *Brunoniella* and *Acanthopale* (Raj 1961; Scotland 1993; Tripp et al. 2013; and additional sampling of limited materials available) varies in size from 40 to ca. 97 µm in diameter (or longest axis), and appears to have fewer than 50 apertures. Palacios Chávez (1975) noted the exceptionally large size of pollen among numerous bat-pollinated or presumably bat-pollinated flowers, including *L. parayi*. Pollen of that species is typical for the genus as a whole, and bat visitation/pollination for species of *Louteridium* is discussed below.

SEEDS.— The relatively large (up to 8 mm long and 6.4 mm wide) seeds are disposed in two rows in each locule of the capsule. Little variation among species was observed for most seed characteristics (Fig. 7). Seeds are discoid (0.40 to 1.23 mm thick) and vary in outline from subcircular to subcordate to subellipsoid. The two flat surfaces vary from smooth to wrinkled and sometimes bear papillae or tubercles, but lack trichomes. Both shape and surface ornamentation sometimes varies within a species. The marginal region is somewhat swollen and the peripheral edge is furrowed and densely pubescent with appressed hygroscopic trichomes. When dry, these trichomes are sometimes inconspicuous and appear as a solid to irregularly eroded peripheral band, but when moistened the trichomes expand to ca. 0.5 mm long (Fig. 7C, K). Most species bear up to 16 seeds per capsule; however, *L. parayi* has up to 18, *L. tamaulipense* has up to 20, and *L. brevicalyx* and *L. rzedowskianum* have up to 24.

CHROMOSOME NUMBERS

No chromosome numbers have been published for *Louteridium*. Among other Trichantherinae, several high numbers (the highest reported for Acanthaceae) have been published for *Sanchezia oblonga* Ruiz & Pav. (n = ca. 66, Grant 1955; $n = 68$, Singh 1951 and Kaur 1970; all reported as *S. nobilis* Hook.f.) and *S. parvibracteata* ($n = 40$, Narayanan 1951; n = ca. 36 to 40, Daniel 2018). Chromosome counts were attempted for several years by Daniel and the late T.I. Chuang for other genera of Trichantherinae, including *Bravaisia* and *Louteridiu*, using techniques noted by Daniel et al. (1984) and Daniel (2018). Conclusive counts from meiotic samples of these genera proved elusive; for the most part, only approximate counts were obtained (Table 2), and even the non-approximate counts noted herein may not represent definitive chromosome numbers for these species. Problems encountered in our cytological studies included: few pollen mother cells (which are very large; cf. Daniel 2018) in each anther; chromosomes irregularly shaped, consisting of distinctly different sizes, and either clumped or otherwise not clearly delimited; apparently

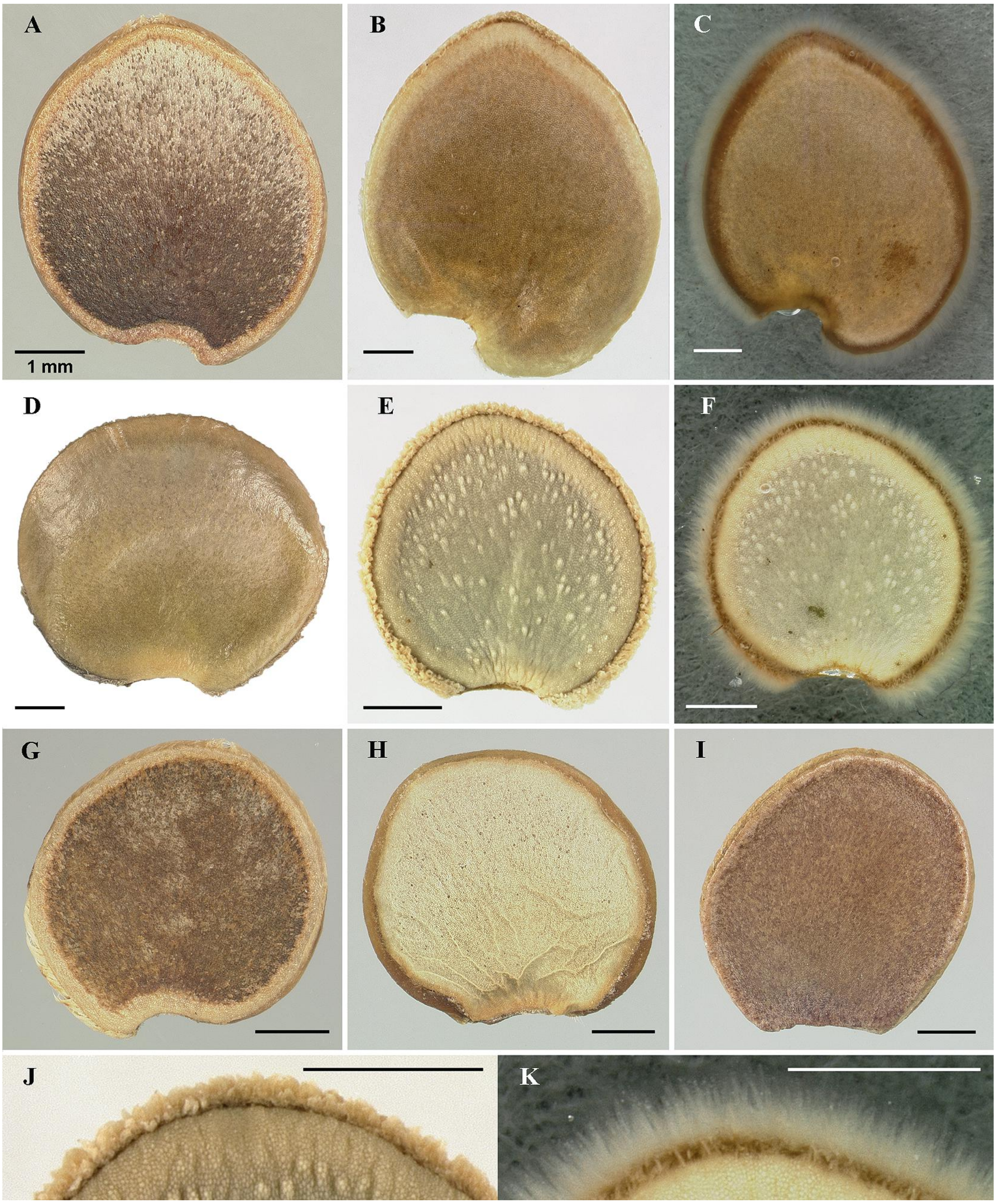


FIGURE 7. Seeds of *Louteridium*. A. *L. donnell-smithii* (*Breedlove & Bourell 68070*). B. *L. brevicalyx* (*Daniel & Steinmann 11913*). C. *L. brevicalyx in water* (*Daniel & Steinmann 11913*). D. *L. dendropilosum* (*Daniel et al. 11784*). E. *L. chartaceum* (*Daniel & Butterwick 5905*). F. *L. chartaceum* (*Daniel & Butterwick 5905*) in water. G. *L. mexicanum* (*Wendt et al. 3614*). H. *L. parayi* (*Breedlove 28970*). I. *L. purpusii* (*Breedlove & Smith 31613*). J. *L. chartaceum* (*Daniel & Butterwick 5905*), detail of dry seed. K. *L. chartaceum* (*Daniel & Butterwick 5905*), detail of seed in water. All scales = 1 mm.

TABLE 2. Approximate meiotic chromosome counts of some Trichantherinae (*Bravaisia*, *Louteridium*, and *Sanchezia*). Herbarium vouchers are at CAS. See text for discussion.

Taxon	n	Location	Collector & Number
Bravaisia berlandieriana	32	BELIZE: Orange Walk	*Daniel 8263*
Bravaisia berlandieriana	29	BELIZE: Orange Walk	*Daniel 8263*
Bravaisia berlandieriana	ca. 26	BELIZE: Corozal	*Daniel 8265*
Bravaisia grandiflora	ca. 44-47	MEXICO: Chiapas	*Daniel & Bartholomew 4998*
Louteridium chartaceum	ca. 24 (-26)	BELIZE: Belize	*Daniel & Butterwick 5905*
Louteridium donnell-smithii	ca. 30	MEXICO: Chiapas	*Breedlove & Daniel 71197*
Louteridium mexicanum	ca. 30	MEXICO: Chiapas	*Breedlove & Daniel 70879*
Louteridium mexicanum	ca. 28 (-30)	MEXICO: Chiapas	*Daniel & Ton 6182*
Sanchezia parvibractetata	ca. 36-40	MEXICO: Chiapas	*Breedlove & Daniel 71315*

conflicting numbers of chromosomes in different cells of the same collection; dark staining cytoplasm; dark staining particles in cytoplasm that do not appear to be either chromosomes or B-chromosomes; and meiotic irregularities (e.g., bivalents aligned in the middle region of a cell and with scattered univalents elsewhere or different numbers of chromosomes per pole in a cell at telophase I). Most counts were made at metaphase I. Like the previously published counts for *Sanchezia*, haploid numbers obtained for *Bravaisia* are relatively high (Table 2). Approximate counts obtained for *Louteridium* (Table 2) are lower numbers (n = ca. 24 to 30), but still somewhat high for Acanthaceae (e.g., Daniel et al. 1984). Using a probable ancestral basic number of $x = 7$ for the family, Daniel (2000) suggested that $n = 68$ for *Sanchezia oblonga* represents cytological evolution to the decaploid level. Although definitive counts for all Trichantherinae and knowledge of chromosome numbers in its sister group(s) will be necessary to propose an ancestral basic number for the subtribe, it appears that included taxa exhibit high chromosome numbers, and that polyploidy and probably also dysploidy were significant in the evolution of taxa in this subtribe.

DISTRIBUTION, ENDEMISM, AND HABITATS

The geographic distribution of *Louteridium* occurs entirely in the northern hemisphere of the Neotropics. Its northern limit (i.e., *L. tamaulipense* in Tamaulipas, Mexico) is 23°07’37.45”N; its southernmost extent (i.e., *L. costaricense* in Chiriquí, Panama) is 08°41’25.09”N; its westernmost occurrence (i.e., *L. koelzii* in Jalisco, Mexico) is 103°28’18.42”W; and its eastern limit (i.e., *L. costaricense* in Guna Yala, Panama) is 078°49’40.88”W. The greatest linear extent of the genus is 2,866 km from west-central Mexico to southeastern Panama. As currently known, the distribution of *Louteridium* is not continuous in Central America. *Louteridium donnell-smithii* occurs as far southeast as western Honduras, and the geographic range of *Louteridium costaricense*, the southernmost-occurring species, occurs from northern Costa Rica to eastern Panama, leaving a gap of approximately 570 km in eastern Honduras and Nicaragua from which no *Louteridium* has been collected. It is possible that *L. costaricense* occurs in southeastern Nicaragua near occurrences in northeastern Costa Rica, but the species has yet to be collected from the former country.

Eight species occur in Mexico, with six of them endemic to that country (Fig. 8). Four of these endemics (*L. brevicalyx*, *L. dendropilosum*, *L. koelzii*, and *L. rzedowskianum*) occur in dry forests of western and southern Mexico on the Pacific versant. The other two Mexican endemics occur in wetter forests of northeastern (i.e., *L. tamaulipense*) and southeastern (i.e., *L. parayi*) Mexico, both on the Gulf of Mexico versant. *Louteridium chartaceum* and *L. costaricense* are both endemic to Central America, with the former restricted to Belize and the latter known only from Costa Rica and Panama. Both of the Central American endemics occur primarily (or exclusively?) on the Caribbean versant. Only three species have relatively broad ranges (i.e., of at least 32,000 km^2), based on extent of occurrences (EOOs; IUCN 2017): *L. costaricense*, *L. mexicanum*, and *L. donnell-smithii* (Figs. 9 to 11). In elevation, *Louteridium* occurs from 1 to 2100 meters, with only one species, *L. donnell-smithii*, spanning that entire range. In general, species of section *Tetrandrium* occur at lower elevations (i.e., 10 to 750 [to 1400] m) than those of sections *Louteridium* and *Parcostamium* (i.e., 1 to 2100 m), but there is significant overlap.

The distributions of two pairs of species are currently known to overlap. Both *L. donnell-smithii* (*Breedlove 50875*) and *L. mexicanum* (*Breedlove & Keller 49526*) occur in northeastern Chiapas, and grow within less than one kilometer of each other. The ranges of *L. mexicanum* and *L. parayi* also overlap, with the EOO of the latter occurring entirely within the EOO of the former. These two taxa have been collected from the same site in the Uxpanapa region of southeastern Veracruz (i.e., *Dorantes 2801* of *L. mexicanum* and *Dorantes 2850* of *L. parayi*), and both species were observed at another site in the Uxpanapa region where *L. parayi* was collected (*Daniel & Wendt 5804*). These same species also occur within less than one km of each other in west-central Chiapas, northwest of Berriozábal (i.e., *Miranda 7834* of *L. parayi* and *Breedlove 24803* of *L. mexicanum*). Although no hybrids between species have been detected among collections examined, considering the interspecific fertility shown for several genera of Acanthaceae (e.g., see partial summary in Daniel 2007), close phylogenetic relationship between *L. donnell-smithii* and *L. mexicanum*, considerable overlap in the flowering seasons for both of these sympatric pairs of species, and likelihood of common pollinators (see below), hybridization between these pairs could be possible.

Although species of *Louteridium* have been reported from several plant communities, it is noteworthy that the sections of the genus recognized here generally correspond to wet vs. dry ecosystems. The six species of sections *Louteridium* and *Parcostamium* all appear to be restricted to moist to wet plant communities. These have been described by collectors as: lowland and montane moist to wet forests (or rain forests), mesophytic montane forests, cloud forests, and tropical semi-evergreen and evergreen forests. In contrast, the five species of section *Tetrandrium* occur in tropical deciduous forests, tropical subdeciduous forests, and evergreen seasonal forests. Among these species, only *L. chartaceum*, which is restricted to steep and well drained limestone hills on the Caribbean coastal plain, occurs in the evergreen seasonal forests (cf. tropical evergreen seasonal broadleaf lowland forests fide Meerman and Sabido 2001). This forest type receives more rainfall than the dry forests in which the other species of section *Tetrandrium* occur. *Louteridium chartaceum* is also the only species of this section that occurs on the Caribbean versant and it is phylogenetically early diverging with respect to other members of its clade (Fig. 1). Thus, it is possible that *L. chartaceum* is somewhat transitional in its habitat between the wet-forest species of sections *Louteridium/Parcostamium* and the four dry forest species of section *Tetrandrium* that occur in western and southern Mexico. Within their respective communities, most data on specimen labels and our observations reveal that species of *Louteridium* generally occur on exposed rocks, rocky slopes, and rocky ground. The exposed rocks or bedrocks are mostly (exclusively?) limestone, commonly with some form of karst topography. Plants frequently occur within riparian zones, but are also found on upland sites not associated with waterways.

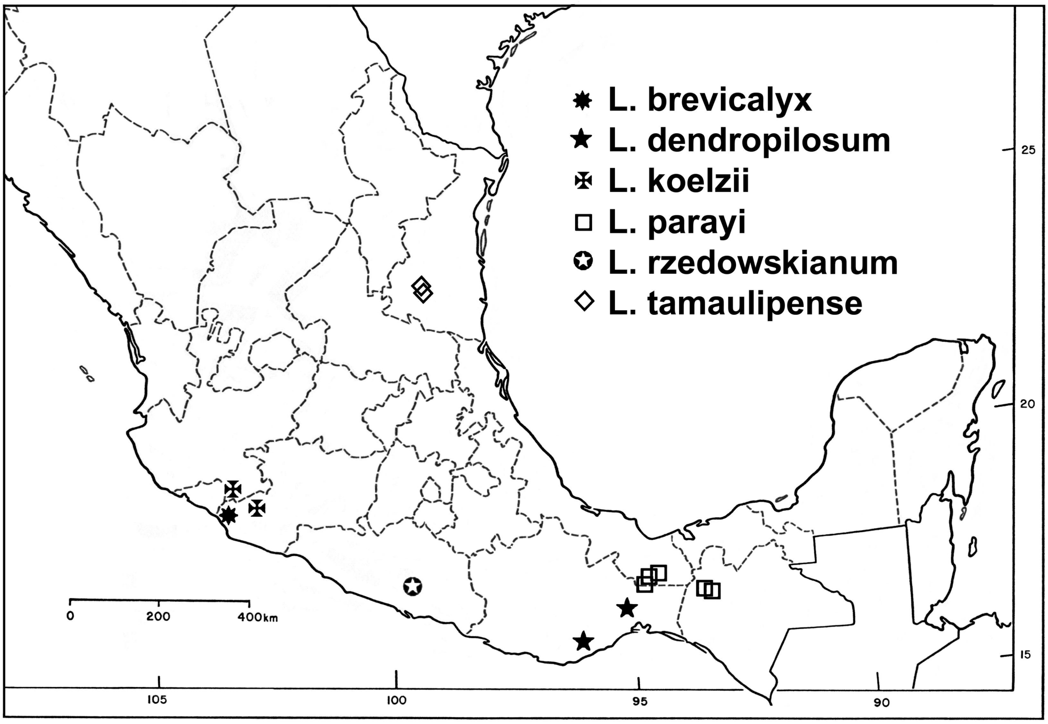


FIGURE 8. Map of Mexico (showing states) and northern Central America with distributions of species of *Louteridium* endemic to Mexico: *L. brevicalyx*, *L. dendropilosum*, *L. koelzii*, *L. parayi*, *L. rzedowskianum*, and *L. tamaulipense*. Symbols may pertain to multiple collections.

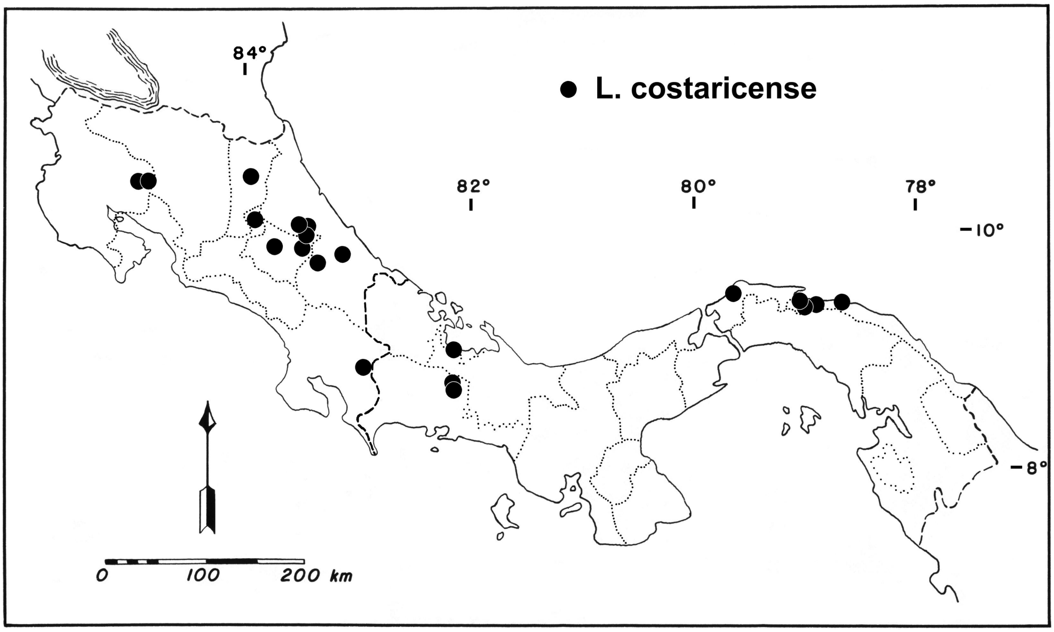


FIGURE 9. Map of Costa Rica (with provinces) and Panama (with provinces and comarcas) with distribution of *Louteridium costaricense*. Dots may pertain to multiple collections.

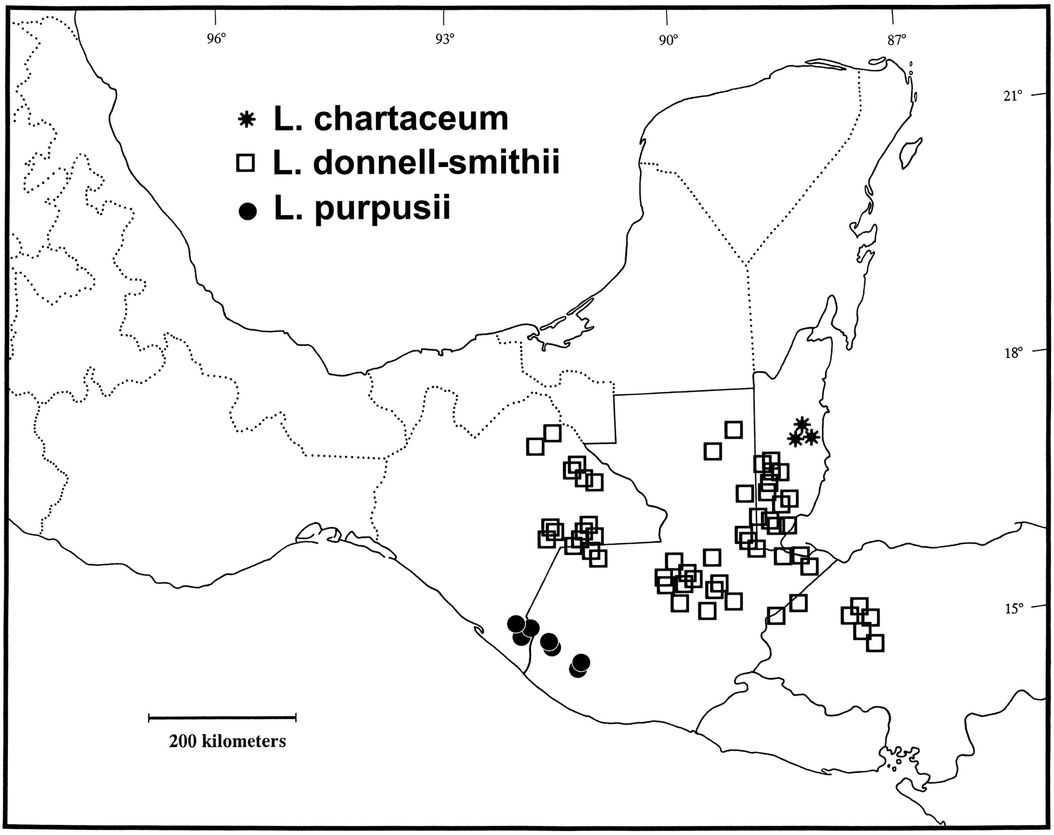


FIGURE 10. Map of southern Mexico (showing states) and northern Central America with distributions of *Louteridium chartaceum*, *L. donnell-smithii*, and *L. purpusii*. Symbols may pertain to multiple collections.

FLORAL ECOLOGY AND REPRODUCTIVE BIOLOGY

Richardson (1972) was able to observe only *L. tamaulipense* in its natural habitat, but he made useful observations on that species. One of us (TFD) located five species in Mexico and Central America and spent varying amounts of time observing each. Plants of four of these (*L. brevicalyx*, *L. chartaceum*, *L. dendropilosum*, and *L. mexicanum*) were subsequently cultivated from seeds or cuttings in San Francisco, California and studied. By the time of this study, three of them had flowered (*L. chartaceum*, *L. dendropilosum*, and *L. mexicanum*), but of these only the latter produced sufficient flowers for most observations and manipulations. Plants of *L. mexicanum* flowered profusely within 12 months of planting. The sole plant of *L. chartaceum* produced only a few large flower buds that abscised prior to opening, and the plant subsequently died. Although multiple plants of *L. brevicalyx* and *L. dendropilosum* have thrived for six years, only a single plant of the latter species began producing an inflorescence in April of 2018, which yielded three flowers in May and June. The following summaries are based on field observations, plants cultivated in San Francisco, information provided by Richardson (1972), and data taken directly from collectors' notes on herbarium specimens. All sources and information specific to the timing of and events during anthesis for species observed in nature/cultivation by us or noted by others is provided in the phenology sections of the species accounts under Taxonomy below.

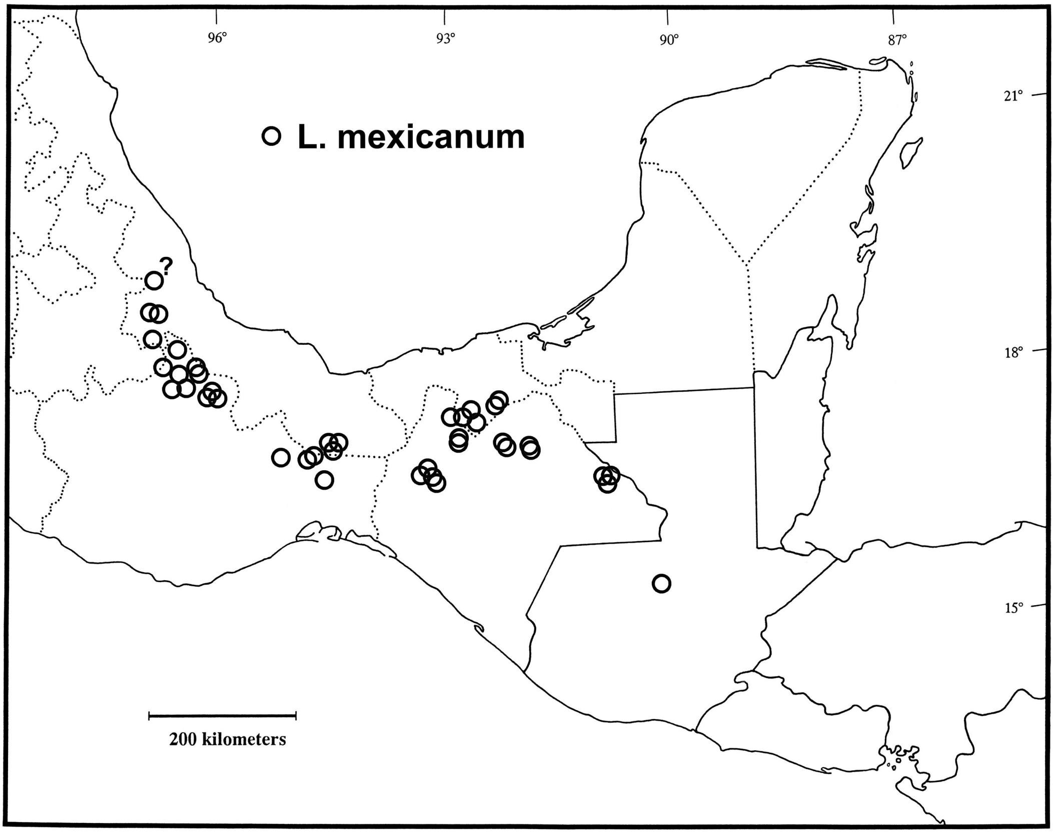


FIGURE 11. Map of southern Mexico (showing states) and northern Central America with distribution of *Louteridium mexicanum*. Circles may pertain to multiple collections.

FLOWERING PHENOLOGY.— Flowering of *Louteridium* occurs throughout the year. Table 3 shows the known months of flowering for each species (i.e., their flowering seasons). It is clear from these data that two phenological patterns are evident among species, corresponding to the sections of the genus. Fruiting periods are noted for each species in the taxonomic accounts below.

Species of section *Tetrandrium*, all of which occur in dry forests, only flower between December and March. These months are in the middle of the dry season (i.e., November to April) along the western and southern coasts of Mexico (Rzedowski 1978) and near the end of the rainy season/first half of the dry season in Belize (Balick et al. 2000). Among species in this section, both *L. brevicalyx* and *L. rzedowskianum* are known from relatively few collections, and it is likely that their respective flowering periods may be somewhat longer than currently known. Flowering during dry seasons is a pattern typical of other Acanthaceae that occur in dry forests of the northern Neotropics (e.g., Daniel 1986, 1990; Tripp 2010; Tripp and Luján 2018).

Species in sections *Louteridium* and *Parcostamium*, all of which occur in moist to wet forests, tend to have longer flowering periods that last either throughout (i.e., *L. costaricense*) or for a greater portion of the year than those of species in section *Tetrandrium*. All of species of sections *Louteridium* and *Parcostamium* flower, or continue flowering, during some or all of the months between June and September, which corresponds to the wettest season in Mexico (Rzedowski 1978) and Central America (Anonymous 2018).

TABLE 3. Known months of flowering for species of *Louteridium* based on herbarium records. The total number of species flowering during each month and the total number of months that each species is in flower are shown. Species marked with "*" pertain to section *Tetrandrium* and occur in dry forests. See text for discussion.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total/Species
*L. brevicalyx**			X										1
*L. chartaceum**	X	X	X										3
L. costaricense	X	X	X	X	X	X	X	X	X	X	X	X	12
*L. dendropilosum**		X	X										2
L. donnell-smithii	X	X	X	X	X	X					X	X	8
*L. koelzii**	X	X										X	3
L. mexicanum	X	X	X	X	X				X	X	X	X	9
L. parayi				X	X	X	X	X	X	X	X	X	9
L. purpusii	X	X	X					X	X	X	X	X	8
*L. rzedowskianum**	X												1
L. tamaulipense			X	X	X	X			X			X	6
Total/Month	7	7	8	5	5	4	2	3	5	4	5	7	

FLORAL LIFE CYCLE, VISITORS, AND POLLINATION.— In general for *Louteridium*, flowers begin to open (i.e., corolla lobes begin to unfurl and separate) in the late afternoon (full opening of individual flowers of *L. dendropilosum* took between 15 and 20 seconds during a series of field observations and up to 25 minutes in a cultivated plant of the species); most or all are fully open by darkness; anthers dehisce promptly and the widely spread stigma lobes are presumably receptive; visitation to flowers occurs soon after the onset of anthesis; and corollas dehisce and fall from the plant by mid- to late- morning of the following day. A corolla, from opening to dehiscing, on a cultivated plant of *L. dendropilosum*, persisted for about 16 hours. At least one variation on this general pattern was noted by Daniel (2010) for a dark colored floral form of *L. donnell-smithii* in Guatemala. If fertilization has been successful, the ovary begins to enlarge within a few days of corolla abscission. The full-sized capsule turns brown prior to maturity, and the mature capsule dehisces explosively, usually within about a month of pollination.

Flowers are borne on relatively long pedicels in inflorescences that are generally located above the leaves. Pollen is located in the dehisced introrse anthers, which are situated several centimeters in front of and usually above the limb of the nototribic corollas. Like the stamens, the style extends in front of (and often slightly above) the corolla, with the stigma located near or up to ca. 1.5 centimeters in front of the anthers. Thus, the front or top of the head or the back of large floral visitors (e.g., bats and possibly hummingbirds) seeking nectar and approaching from the front of the flower could readily make contact with both the stigma (first) and anthers (second).

Diurnal visitors to flowers include hummingbirds, which probe for nectar, and small bees or flies, which were only observed visiting anthers. Unidentified hummingbirds were observed visiting flowers of *L. tamaulipense* in the early morning (Richardson 1972), and a Cinnamon Hummingbird (*Amazilia rutila*) was observed probing inside flowers of *L. dendropilosum* during the late afternoon (before dusk), following anthesis of at least some flowers during daylight hours.

Nocturnal visitors include bats and moths (e.g., F. Archila, in litt.; see phenology section under *L. donnell-smithii* below). Characteristics of flowers associated with pollination by bats in the Neotropics have been summarized by numerous authors (e.g., Pijl 1957; Vogel 1969b; Proctor and Yeo 1972; Cruden et al. 1983; Baker et al., 1998; Willmer 2011; Abrol 2012). Plants of *Louteridium* share most of these attributes, including: tree-like or epiphytic habit (most species), inflorescences/flowers produced free from the foliage (inflorescences generally borne above the vegetative shoots, which in some species are leafless during the flowering season, and flowers borne on elongate pedicels), nocturnal anthesis (currently documented for most species), drab flower color (corollas mostly greenish, yellowish, white, or sometimes chestnut to maroon), large flowers (corollas 35 to 72 mm long), corolla open bowl- or bell-shaped (bell-shaped with a wide mouth and a saccate throat), large anthers (6.5 to 17 mm long), large pollen grains (106 to 143 μm in diameter), and an abundance of hexose-rich nectar (see discussion below). One characteristic often associated with chiropterophily is a musky or mouse-like odor, dominated by sulphur-containing compounds (e.g., Knudsen and Tollsten 1995). No odor was detected for *Louteridium* among living flowers observed or noted among collectors' data on herbarium labels. Pollination of Neotropical Acanthaceae by bats has been documented for *Trichanthera gigantea* (Acanthoideae: Ruellieae: Trichantherinae; Steiner 1981; Anonymous 1984; and see discussion in Daniel 2015), *Harpochilus neesianus* (Acanthoideae: Justicieae; Vogel et al. 2004), and *Aphelandra acanthus* Nees (Acanthoideae: Acantheae; Muchhala et al. 2009). Flowers of other Acanthaceae that share some or all floral adaptations associated with bat pollination have been noted for some species of *Ruellia* section *Chiropterophila* (e.g., Palacios Chávez 1975; Ramamoorthy and Lorence 1987; Ramamoorthy 1991; Tripp and Manos 2008; Tripp 2010).

Species of *Louteridium* that have been noted as likely pollinated by bats include *L. chartaceum* and *L. donnell-smithii* (e.g., Vogel 1969a; Fleming et al. 2009) and *L. parayi* (Palacios Chávez 1975). Based on the preponderance of evidence from floral morphological characteristics, timing of anthesis, nectar quantity and sugar composition, and observations on floral visitors, it would appear that flowers of all species of the genus are well adapted for, and undoubtedly pollinated by, Neotropical bats (Microchiroptera). *Louteridium* appears to be the largest genus of Acanthaceae entirely adapted for pollination by bats. Diurnal visits by hummingbirds have been noted to other chiropterophilous flowers of Acanthaceae (e.g., Tripp et al. 2013) and of other families (e.g., Abrol 2012). It is likely that hummingbirds that visit flowers of *Louteridium* also play a role in their pollination.

Floral Rewards/Nectar.— Flowers of two species (*L. dendropilosum*, *L. tamaulipense*) were noted to lack any discernable scent (Richardson 1972; TFD, personal observations). However, flowers of *Louteridium* present floral visitors with at least two potential rewards, pollen and nectar. The locations on the flowers of both are discussed above (see Morphology). Visitors to flowers of *Louteridium* noted above include small bees or flies, hummingbirds, and bats. Small bees and flies were only observed gathering pollen from anthers, and did not make contact with other parts of the flower, whereas both hummingbirds and bats were observed either visiting and/or interacting with the corolla as well as the reproductive structures.

Quantities of nectar present in flowers vary among species. Richardson (1972:64) indicated that there was "not an abundance" of nectar in flowers of *L. tamaulipense* that he examined in the field. Similarly, no nectar was observed in newly opened or post-mature flowers of either *L. dendropilosum* or *L. brevicalyx* in their native habitats. However, it is probable that nectar was present in corollas of these flowers, but obscured from view by the filament curtain (see Morphology above). Indeed, abundant floral nectar (78.6 μl) in a cultivated plant of *L. dendropilosum* (*Daniel et al. 11894cv*), while not visible because of the invaginations of the corolla and filament curtain (Fig. 2L), was located by probing through these obstacles with a micropipette. This situation in somewhat similar to corollas of *Ruellia conzattii* Standl. and *R. laslobasensis* E. Tripp, which can have large quantities of nectar hidden by the filament curtain. By contrast, a plant of *L. mexicanum* (*Breedlove & Daniel 70879gh*) cultivated in a greenhouse in San Francisco formed pools of nectar in the anterior portion of the saccate throat of the corolla tube. In these flowers visible nectar extends along the trough formed by the lateral invaginations in the anterior portion of the throat (see Morphology above). Standing crop nectar volumes in three flowers of this plant of *L. mexicanum* were 145.6 µl, 184.4 µl, and 197.6 µl (mean = 175.9; SD = 27.0). These amounts are comparable to quantities present in other bat-adapted species of Acanthaceae, such as *Ruellia malaca* (up to 180 µl; Tripp and Luján 2018), *R. conzattii* (432 µl; Daniel unpublished), and *R. laslobasensis* (168 µl; Daniel unpublished).

Nectar quality for *L. mexicanum* and *L. parayi*, expressed here by the ratios of the relative percentages of sucrose to hexose sugars (i.e., glucose + fructose), was determined by C.E. Freeman using high-performance liquid chromatography (HPLC), the methodology of which was outlined by Ellisens and Freeman (1988), with modifications noted in Freeman et al. (1991). The results of multiple samples of a single collection for each species are shown in Table 4. Baker and Baker (e.g., 1983, 1990) demonstrated correlations between sucrose:hexose ratios and pollinator types for numerous groups of plants. Nectar sugar ratios of Acanthaceae studied to date (e.g., Baker et al. 1998; Daniel 1986, 1990; Holmqvist et al. 2005; Freeman 1986; Freeman et al. 1991; Daniel and Freeman, unpublished data) generally conform to these sugar preference correlations. Table 4 shows that sampled nectar profiles of *L. mexicanum* and *L. parayi*, species representative of two of the three sections of the genus, pertain to the "hexose-rich" category (i.e., S/G + F ranging from 0.1 to 0.49; Baker and Baker 1983). Neotropical flowers visited/pollinated by bats are consistently hexose-rich or hexose-dominant (Baker and Baker 1983). By contrast, hummingbird visited/pollinated flowers generally offer sucrose-rich nectar (i.e., S/G + F ranging from 0.5 to 0.99; Baker and Baker 1983). Thus, based on our sampling, flowers of *Louteridium* have both floral morphological traits and nectar sugar chemistry that strongly suggest adaptations for pollination by bats. Hummingbirds may be opportunistic visitors to these flowers during daylight hours, when bats are generally not present, and likely also serve as pollinators.

TABLE 4. Nectar sugar composition of samples from five flowers of *Louteridium mexicanum* (*Breedlove & Daniel 70879cv*, grown from seed in a greenhouse) and three flowers of *L. parayi* (*Daniel & Wendt 5805*, from plants in their native habitat). Percentages of the hexose sugars fructose (F) and glucose (G) are compared to the percent of sucrose (S). Sample means (*µ*) and sample standard deviations (s) for percentages and ratios are shown. Samples were analyzed by C.E. Freeman using High Performance Liquid Chromatography.

***L. mexicanum* samples**	**%F**	**%G**	**%S**	**S:F+G**
1	32.4	39.5	28.1	0.39
2	33.7	44.3	22.0	0.28
3	34.4	44.1	21.5	0.27
4	32.5	39.7	27.8	0.39
5	32.2	44.2	23.6	0.31
µ	33.0	42.4	24.6	0.33
s	1.0	2.5	3.2	0.06
***L. parayi* samples**				
1	34.4	42.0	23.6	0.31
2	33.9	42.9	23.2	0.30
3	34.4	42.0	23.6	0.31
µ	34.2	42.3	23.5	0.31
s	0.3	0.5	0.2	0.00

SELF-COMPATIBILITY, AUTONOMOUS AGAMOSPERMY, AND VEGETATIVE PROPAGATION.— Experiments and observations to determine self-compatibility and at least one form of asexual reproduction were undertaken on flowers of a greenhouse-cultivated plant of *Louteridium mexicanum* (*Breedlove & Daniel 70879gh*) in March of 1990. Over several weeks, varying numbers (n) of flowers were marked for each of the following treatments: control (n = 13, no treatment), emasculation (n = 10, anthers excised prior to dehiscence), and artificial self-pollination (n = 22, anthers excised prior to dehiscence and stigma manually dusted with pollen after dehiscence of anthers). Fruit-set was used as a measure of fertilization and self-compatibility.

The greenhouse studies reveal that, like most Acanthaceae studied to date (e.g., Daniel 1993 and additional unpublished data), *L. mexicanum* is self-compatible; of the 22 self-pollinated flowers, 17 set fruit (77%). None of the emasculated flowers set fruit, which strongly suggests that autonomous agamospermy does not occur in this species. Two of the 13 control flowers (15%) set fruit. Although neither bats nor birds had access to the plant studied, other potential pollinators were not specifically excluded in the greenhouse. Thus, whether the control flowers that set fruit resulted from pollination by a floral visitor or via autogamy remains unknown. The presence of pollinators in the greenhouse, if any, would not appear to have been pervasive because none of the 10 emasculated flowers set fruit.

It is worth noting that although asexual reproduction via autonomous agamospermy was not shown to occur in *Louteridium mexicanum*, vegetative propagation via fragmentation was noted to occur in this and two other species. One of the plants of *L. dendropilosum* cultivated from seed rotted at the base. Prior to the death of this plant, the apical two to four centimeters of six branch stems were excised and partially buried in potting soil. All six cuttings grew into healthy plants. Additionally, cuttings made in the field of both *L. chartaceum* and *L. mexicanum* were subsequently planted and successfully cultivated in San Francisco, California. The degree to which sexual reproduction vs. reproduction via fragmentation is important to natural populations remains unknown.

Floral Abscission, Pollen Viability, and Stigma Receptivity.— Observations of *Louteridium mexicanum* grown in a greenhouse (*Breedlove & Daniel 70879gh*) revealed that unpollinated flowers abscise from the plant (thus terminating anthesis of those flowers) on the morning of the second day the flowers are open. Abscission of the entire flower and pedicel occurs at or near the base of the pedicel (vs. corolla with epipetalous stamens falling first from the flower in most other Acanthaceae). It was also observed that manually self-pollinated flowers generally do not abscise (although the corolla eventually either falls or withers), but continue developing toward fruit-set. Thus, floral abscission was used to test whether pollination is more effective during the evening of day 1 (at the commencement of anthesis) or during the morning of day 2 (ca. 15 hours later, but prior to floral abscission). Isolated flowers were marked and treated as shown in Table 5.

Table 5. Efficacy of pollination at different times in the floral life-cycle of *Louteridium mexicanum* based on floral abscission. See text for discussion.

Treatment	No. Tagged	No. Abscised
Control (no manual self-pollination)	10	10
Selfed on evening of day 1	10	2
Selfed on morning of day 2	8	2

From this experiment, it would appear that, in most instances the pollen is viable and the stigma is receptive for most or all of the time that flowers typically remain on the plant. Thus, both diurnal and nocturnal pollinators could be effective ones. Fruit-set, which only occurs when embryos develop in Acanthaceae, was not determined for the self-pollinated and retained flowers in this experiment. It remains to be determined whether abscission at or near the base of the pedicel of non-pollinated flowers is widespread, and thus possibly synapomorphic, for species of *Louteridium*. Somewhat similar abscission was observed (by TFD) in cultivated plants of two species of *Ruellia* (*R. conzattii* and *R. laslobasensis*), both of which have mostly nocturnal flowers with corollas that are somewhat similar to those of *Louteridium* in size, shape, and coloration. However, in these two species, floral abscission occurs at the base of the calyx, between two and four days after earlier abscission of the corolla.

CONSERVATION

Walter and Gillett (1998) listed *L. chartaceum* and *L. mexicanum* as rare, and *L. rzedowskianum* (as "L. rzedowskii") as endangered**.** Data pertinent to conservation and preliminary conservation assessments, based on more recent IUCN (2017) guidelines, are here provided for all 11 species of *Louteridium*. For each species, the presence of protected areas within their respective extent of occurrence (EOO; calculated using Google Earth Pro, 2018) is summarized, and the known occurrences of species in protected areas are also indicated. Protected areas noted in the discussions include international, national, natural, and pertinent state/municipal parks; biosphere reserves; forest/nature reserves; field/research stations; formally protected biotopes and archeological sites; conservation centers; and wildlife sanctuaries. The inclusion of species in these areas is based on information from specimen labels and/or georeferenced collection data that show presence of occurrences within the boundaries of such areas.

Based on EOO calculations, six species (*L. brevicalyx*, *L. chartaceum*, *L. dendropilosum*, *L. koelzii*, *L. rzedowskianum*, and *L. tamaulipense*) are known from limited geographic ranges of less than 200 km^2. One of these, *L. rzedowskianum*, is known only from the type locality, from which it was collected twice over a period of eight years. Two species (*L. parayi* and *L. purpusii*) have EOO's between 900 and 2,500 km^2; and three species (*L. costaricense*, *L. donnell-smithii*, and *L. mexicanum*) have relatively large distributions with EOO's between 32,500 and 62,000 km^2. Threats to species and/or reductions in populations, where known or perceived, are discussed in the taxonomic treatment below.

The preliminary conservation assessments proposed here can be summarized as: Data Deficient (*L. rzedowskianum*), Least Concern (*L. costaricense*, *L. donnell-smithii*, *L. mexicanum*), Near Threatened (*L. tamaulipense*), Endangered (*L. chartaceum*, *L. dendropilosum*, *L. koelzii*, *L. parayi*, *L. purpusii*), and Critically Endangered (*L. brevicalyx*). Thus, six of the 11 species appear to pertain to a threatened category.

TAXONOMY

Louteridium S. Watson, Proc. Am. Acad. 23:283. 1888. **Type.**— *Louteridium donnell-smithii* S. Watson. [from Greek, *luterion*, a washing basin on a pedestal, and diminutive suffix, *-ium*, in reference to the form of the corolla]

Neolindenia Baill., Bull. Mens. Soc. Linn. Paris 2:851. 1890. **Type.**— *Neolindenia mexicana* Baill. (≡ *Louteridium mexicanum* (Baill.) Standl.).

Terrestrial, epiphytic, or epipetric (perennial herbs) shrubs or usually trees to 12 m tall and 25 cm dbh (sometimes multi-trunked and/or with prop roots) bearing cystoliths. Leaves seasonally deciduous (i.e., leafless for part of the year) or persistent (some leaves always present), clustered at shoot apex or distributed ± evenly along new growth, opposite (often appearing quaternate when clustered), petiolate (to subsessile), petioles often tinged with pink or red, blades membranaceous to subsucculent, midvein (and secondary veins) often red or pinkish, margin entire to crenate-dentate. Inflorescence a terminal open or contracted raceme to thyrse (or modifications thereof, see discussion in Morphology above); dichasia opposite or alternate, sessile to pedunculate, subtended by a bract, 1–many-flowered, often expanded and appearing like a lateral branch. Bracts (i.e., along primary rachis) opposite, green, often caducous, margin entire (to subcrenate). Bracteoles (i.e., subtending floral pedicels and lateral branches, when present, of dichasia) often caducous, those of a pair homomorphic. Flowers homostylous, long-pedicellate. Calyx deeply 3-lobed (or 5-lobed with 3 prominent lobes and 2 reduced lobes in some presumably teratological calyces of *L. brevicalyx*; see discussion under that species), sometimes ± accrescent in fruit, lobes subhomomorphic to heteromorphic, posterior lobe conduplicate or planar, larger or smaller than lateral lobes, subsaccate or with a flap at base only in *L. parayi*, lateral lobes planar. Corolla white, greenish, or yellow (and often tinged with maroon), or dark chestnut to maroon, or brownish, relatively large, tube abruptly expanded into an obliquely bell-shaped and anteriorly saccate throat, narrow proximal portion of tube (i.e., from base of corolla to point of insertion of stamens) ± cylindric, limb subbilabiate, upper lip 2-lobed, lower lip 3-lobed, lobes subequal, often recurved to recoiled, entire to 2-fid at apex, contorted in bud. Stamens 2 (usually accompanied by 2 staminodes near base) or 4 (with 1 staminode, or staminode either absent or not evident), filaments inserted at or near base of corolla throat (i.e., at or several mm distal to apex of narrow proximal portion of corolla tube), usually long-exserted from mouth of corolla, glabrous or usually pubescent proximally with eglandular trichomes, anthers 2-thecous, thecae elongate, equal in size, parallel to sagittate, equally inserted, lacking basal appendages, dehiscing toward lower lip (i.e., flower nototribic), glabrous; pollen spheric to subspheroidal, pantoforate with apertures > 50, exine gemmate to baculate and with additional sparse to dense microsculpturing; staminodes (if present or evident) usually consisting of inconspicuous subulate to triangular projections (rarely an elongate sterile filament in section *Tetrandrium*). Style usually long-exserted from mouth of corolla, stigma 2-lobed and sometimes ± funnelform, lobes usually ± flattened, equal to unequal in size. Nectar disk prominent below gynoecium, up to 3 mm high, annular or ± cupulate. Capsules substipitate to stipitate, relatively large, head ovoid to ellipsoid to linear-ellipsoid, septa with attached retinacula remaining attached to inner wall of mature capsule. Seeds up to (12) 16 (24) per capsule, disposed in 2 rows in each locule, discoid, subcircular to subcordate to subellipsoid in outline, flat surfaces smooth to wrinkled and sometimes with papillae or tubercles, lacking trichomes, marginal region ± swollen, peripheral edge ± furrowed and densely pubescent with appressed hygroscopic trichomes.

This genus of 11 species occurs in either seasonally dry or moist to wet regions from northeastern Mexico (southern Tamaulipas) to eastern Panama (central Guna Yala). Nine species are known from Mexico, with six endemic there. Several of the Mexican species are known from either few collections and/or have very restricted distributions within the country. Five species occur in Central America with one endemic to Belize, and another restricted to Costa Rica and Panama. El Salvador and Nicaragua are the only nations in Central America from which the genus is not currently known to occur.

The three sections of *Louteridium* treated here correspond to the three clades revealed by molecular sequence data (Fig. 1). One of these, section *Parcostamium*, has not been previously recognized, and is based largely on molecular characters. Basic taxonomic information for each section and a validating protologue for section *Parcostamium* are provided below. The three sections are also referenced in the key to species.

1. ***Louteridium* section *Louteridium***. Type.— *Louteridium mexicanum* (Baill.) Standl.

Evergreen shrubs or trees (to 12 m tall); herbaceous stems glabrous or puberulent to pubescent with eglandular (and rarely also glandular) trichomes; leaves not seasonally/simultaneously deciduous, membranaceous, ± evenly distributed along stems; calyx 17–40 mm long (during anthesis); stamens 2.

The three species of this section (*L. donnell-smithii*, *L. mexicanum*, and *L. purpusii*) occur from southern Mexico (central Veracruz) into western Honduras (west-central Comayagua).

2. ***Louteridium* section *Parcostamium*** T.F. Daniel & E. Tripp, sect. nov. Type.— *Louteridium costaricense* Radlk. & Donn. Sm.

Evergreen perennial herbs, shrubs, or small trees (to 3 m tall); herbaceous stems glabrous; leaves not seasonally/simultaneously deciduous, subsucculent, ± evenly distributed along stems; calyx 23–65 mm long (during anthesis); stamens 2.

The three species of this section (*L. costaricense*, *L. parayi*, and *L. tamaulipense*) together span the entire geographic range of the genus, and contain both the northern- and southern-most occurring species. These species do not appear to share morphological characteristics that are not otherwise found among species in other sections. Section *Parcostamium* differs from section *Tetrandrium* by having two (vs. four) stamens, leaves that are ± evenly distributed along stems (vs. clustered near apex) and are not seasonally/simultaneously deciduous (vs. seasonally deciduous), and generally longer calyces (23 to 65 vs. 5 to 32 mm). It differs from section *Louteridium* by its generally smaller habit (perennial herbs, shrubs, or small trees to 3 m tall vs. shrubs to trees to 12 m tall); leaf texture (subsucculent vs. membranaceous); and generally shorter pedicels (up to 58 vs. up to 95 mm long). The sectional name is derived from the first three letters of all species included in the section.

3. ***Louteridium* section *Tetrandrium*** A. Richardson. **Type**.— *Louteridium chartaceum* Leonard.

Deciduous shrubs or trees (to 12 m tall); herbaceous stems lacking trichomes or pubescent with dendritic eglandular trichomes; leaves seasonally/simultaneously deciduous, membranaceous to subsucculent, clustered near apex of stems; calyx 5–32 mm long (during anthesis); stamens 4.

The five species of this section (*L. brevicalyx*, *L. chartaceum*, *L. dendropilosum*, *L. koelzii*, and *L. rzedowskianum*) occur from west-central Mexico (Jalisco) to east-central Belize (Belize).

Key to Species of *Louteridium*

1a. Stamens 4; leaves ± clustered on stems, seasonally deciduous (i.e., plants leafless for part of the year); occurring in dry, deciduous or subdeciduous forests. . . . . Sect. *Tetrandrium*

  2a. Calyx 5–9 mm long, lobes 3.5–4.8 mm long, posterior lobe broadly ovate to subtriangular; Guerrero . . . . *L. rzedowskianum*
  2b. Calyx 10–32 mm long, lobes 7.5–32 mm long, posterior lobe linear to lanceolate to ovate to subelliptic to subrhombic-obovate.

    3a. Dendritic trichomes present on vegetative and reproductive structures; inflorescence a raceme (i.e., dichasia sessile); Oaxaca . . . . *L. dendropilosum*
    3b. Dendritic trichomes absent on vegetative and reproductive structures; inflorescence usually a thyrse (i.e., dichasia usually pedunculate); western Mexico (Jalisco and Michoacán) or Belize.
      4a. Calyx 10–16 mm long, lobes 7.5–12 mm long; corolla externally pubescent with glandular and eglandular trichomes; inflorescence rachis pubescence including glandular trichomes; capsule 32–42 mm long, pubescent with eglandular and glandular trichomes; style 75–77 mm long; seeds 16–24 per capsule; Michoacán. . . . . *L. brevicalyx*
      4b. Calyx 17–28 mm long, lobes 15–37 mm long; corolla externally glabrous; inflorescence rachis glabrous or pubescent with eglandular trichomes only; capsule (20–) 23–30 mm long, glabrous or pubescent with eglandular trichomes only; style 50–67 mm long; seeds up to 16 per capsule.

5a. Inflorescence rachis, peduncles, and pedicels glabrous; calyx lobes linear to lance-linear, 3–5 mm wide; corolla 35–40 mm long; stamens 55–77 mm long, thecae 6.5–9.5 mm long; capsules glabrous; Belize . . . . *L. chartaceum*

5b. Inflorescence rachis, peduncles, and pedicels pubescent with eglandular trichomes; calyx lobes ovate-elliptic to elliptic to obovate, 9–15 mm wide; corolla 50–55 mm long; stamens 72–90 mm long, thecae 10–12 mm long; capsules pubescent; western Mexico (Jalisco and Michoacán). . . . . *L. koelzii*

1b. Stamens 2; leaves ± evenly distributed along young stems, not all seasonally deciduous (i.e., plants never entirely leafless); occurring in moist to wet forests. . . . . Sects. *Louteridium* and *Parcostamium*

6a. Leaf blades oblanceolate to obovate; inflorescence appearing conspicuously dichotomously branched; bracteoles of a pair connate along one side for up to 1/2 their length and subsaccate at base; posterior lobe of calyx subsaccate or with a flap-like appendage at base; corolla externally glabrous; capsule glabrous; Mexico. . . . . *L. parayi*

6b. Leaf blades cordate to ovate to broadly ovate to elliptic to broadly elliptic to obovate; inflorescence not appearing dichotomously branched; bracteoles neither connate nor subsaccate; posterior lobe of calyx not subsaccate/appendaged at base; corolla externally pubescent; capsule pubescent (glabrous in *L. costaricense*); Mexico and Central America.

7a. Bracts persistent during flowering; capsule glabrous, stipe 7–12 mm long; southern Central America (Costa Rica and Panama). . . . . *L. costaricense*

7b. Bracts caducous during flowering (or sometimes proximal bracts persisting in *L. donnell-smithii*); capsule with sessile or stipitate glands, stipe 1–4 mm long; Mexico and northern Central America.

8a. Leaves subsucculent; posterior calyx lobe planar; style 48–73 mm long, seeds up to 20 per capsule; northeastern Mexico (Tamaulipas). . . . . *L. tamaulipense*

8b. Leaves membranaceous; posterior calyx lobe conduplicate; style 72–92 mm long; seeds up to 16 per capsule; southern Mexico, Belize, Guatemala, and western Honduras. . . . . Sect. *Louteridium*

9a. Young stems and leaves densely pubescent with erect to flexuose eglandular trichomes to 2 mm long; inflorescence peduncles and rachis, flower pedicels, and abaxial surface of calyx pubescent with glandular and eglandular trichomes to 2.8 mm long (viscid); leaf margin crenate-dentate. . . . . *L. donnell-smithii*

9b. Young stems and leaves glabrous or pubescent with erect, flexuose, retrorse, or antrorse eglandular trichomes < 0.05–0.5 mm long; inflorescence peduncle and rachis, flower pedicels, and abaxial surface of calyx glabrous or pubescent with eglandular trichomes < 0.05–1 mm long; leaf margin entire to crenate (sometimes to crenate-dentate in *L. mexicanum*).

10a. Rachis glabrous or pubescent with flexuose to flexuose-antrorse trichomes 0.2–1 mm long (villous); pedicels glabrous or villous; abaxial surface of calyx either appearing glabrous (although covered with glandular punctations < 0.05 mm in diameter) or villous along keel; capsule sparsely puberulent with sessile to subsessile glands to 0.05 mm long; leaf blades broadly ovate to ovate to elliptic to broadly elliptic; Gulf of Mexico and Caribbean Sea versants . . . . *L. mexicanum*

10b. Rachis puberulent with (retrorse to) erect to flexuose to antrorse trichomes to 0.05 mm long; pedicels puberulent with erect to retrorse (to antrorse) trichomes to 0.05 mm long; abaxial surface of calyx pubescent like pedicels and sometimes with a few sparse glandular trichomes to 0.2 mm long as well; capsule densely pubescent with glands (0.05–) 0.1–0.4 mm long; leaf blades ovate-elliptic to obovate-elliptic to obovate; Pacific versant . . . . *L. purpusii*

1. *Louteridium brevicalyx* A. Richardson, *Tulane Stud. Zoo. Bot.* 17:66. 1972. **Type**.— MEXICO. **Michoacán**: Distr. Coalcomán, Aquila [ca. 18°35’49.39”N, 103°30’14.64”W], 200 m, 21-III-1941 (flr, frt), *G. Hinton et al. 15825* (holotype: US!; isotype: NY!).

Trees to 8 m tall, mostly epipetric. Older (woody) stems subquadrate to terete, irregularly fissured, sometimes ± scurfy, often lenticellate, lacking trichomes; younger (herbaceous) stems terete (when fresh), becoming flattened on drying, sparsely lenticellate, irregularly fissured, lacking trichomes. Leaves seasonally deciduous, clustered at shoot apex, petiolate, petioles to 90 mm long, sometimes tinged with pink or red, blades subsucculent, narrowly ovate to ovate to elliptic, 85–157 mm long, 31–76 mm wide, 1.8–2.7 × longer than wide, acute to acuminate at apex, acute to attenuate at base, surfaces glabrous (or rarely with very few scattered flexuose eglandular trichomes mostly on veins on abaxial surface, the trichomes especially evident on immature leaves), midvein sometimes pinkish to reddish purple (especially adaxially), margin entire. Inflorescence a terminal sessile or pedunculate thyrse to 38 cm long (including peduncle, if present, and excluding corollas), peduncle (if present) pubescent with erect to flexuose glandular trichomes 0.05–0.7 mm long (glandular pubescent), rachis glandular pubescent and often with scattered erect to flexuose eglandular trichomes to 0.7 mm long as well; dichasia opposite or alternate, pedunculate, 1–many-flowered, to 120 mm long (excluding corollas), dichasial peduncles 15–60 mm long, pubescent like rachises. Bracts caducous (rarely present), lanceolate to lance-ovate, 6.5–7.5 mm long, 2.5–2.8 mm wide, abaxially pubescent like rachis (except sometimes with more eglandular trichomes). Bracteoles and secondary bracteoles caducous, lance-subulate to linear to ovate-elliptic, 2–7 mm long, 0.9–2 mm wide, abaxially pubescent like rachis or with more eglandular trichomes. Flowers pedicellate, pedicels 25–50 mm long, glandular pubescent. Calyx 10–16 mm long, lobes fused at base for 1.5–3 mm, subhomomorphic to subheteromorphic, membranaceous, lanceolate to ovate, 7.5–12 mm long, 3–7 mm wide, subequal or with posterior lobe either slightly larger or smaller than lateral lobes, acute at apex, abaxially pubescent with erect to flexuose glandular and eglandular trichomes 0.05–0.3 mm long, posterior lobe subplanar to subconduplicate. Corollas greenish, 35–65 mm long, externally pubescent with erect to flexuose glandular and eglandular trichomes 0.05–0.3 mm long, tube 25–30 mm long, narrow proximal portion 7–12 mm long, 7–11 mm in diameter near midpoint, throat 15–25 mm long, 26–30 mm in diameter at mouth, lobes spreading to recoiled, ovate to subcircular, 15–24 mm long, 16–24 mm wide, rounded and emarginate at apex. Stamens 4, 65–80 mm long, filaments distally glabrous, pubescent with eglandular trichomes near base, thecae 8–11 mm long; staminode 0. Style 75–77 mm long, glabrous distally, pubescent near base with eglandular trichomes, stigma subequally 2-lobed and ± funnelform, lobes elliptic to subspheric, 2–3 mm long, 1.5–3 mm wide. Capsules 32–42 mm long, 6–9.5 mm in diameter, pubescent with erect to flexuose eglandular and subsessile to stipitate glandular trichomes less than 0.05–0.4 mm long, stipe 2–5.2 mm long. Seeds 16–24 per capsule, 5.5–7 mm long, 4.5–6 mm wide, surfaces smooth.

Phenology.— Flowering: March; fruiting: March. Field observations on *Daniel & Stein-*

mann 11913 reveal that no flowers were open between 16:00–17:30 on the first day of observations, but several very large floral buds were present. On the following day, all of the large buds were found to be fully open at 08:30, and no visitors were noted over the course of an hour.

Distribution and habitat.— West-central Mexico (Michoacán; Fig. 8); plants occur on exposed limestone, often on steep slopes of arroyos, in tropical subdeciduous forests at elevations from 200 to 590 meters.

Illustrations.— Figure 2A–E; Richardson (1972:66, fig. 2).

Conservation.— Except for *L. rzedowskianum*, which is known from a single site, *L. brevicalyx* has the smallest known EOO (0.27 km^2) among its congeners. At the site of *Daniel & Steinmann 11913*, about 100 plants were seen growing, mostly epipetrically, in an area of ca. 5000 m^2 on exposed limestone slopes in forest. No protected land appears to be within the species EOO. Evident threats to this species appear to be large-scale mining in the vicinity of *Daniel & Steinmann 11913* (ca. 1.5 km distant) and deforestation for agriculture (including cattle) that is evident within the small EOO and in adjacent regions. Given the size of the EOO and apparent major threat (i.e., deforestation for agriculture), a single location is evident. A preliminary conservation assessment of Critically Endangered (CR; B1, a, b; IUCN 2017) is proposed for *L. brevicalyx*.

Discussion.— Leaves are absent on the field specimens examined. Information on young stems and leaves provided above is from cultivated plants (*Daniel & Steinmann 11913cv)*. Leaves of these plants may not have attained the maximum size encountered in natural settings. The inflorescence, which appears before the leaves, arises from the apex of the previous season's woody growth and bears a stalked (pedunculate) thyrse or a sessile rachis subtended by axillary dichasia (sessile thyrse). A stem forms with the flush of new clustered leaves later in the season.

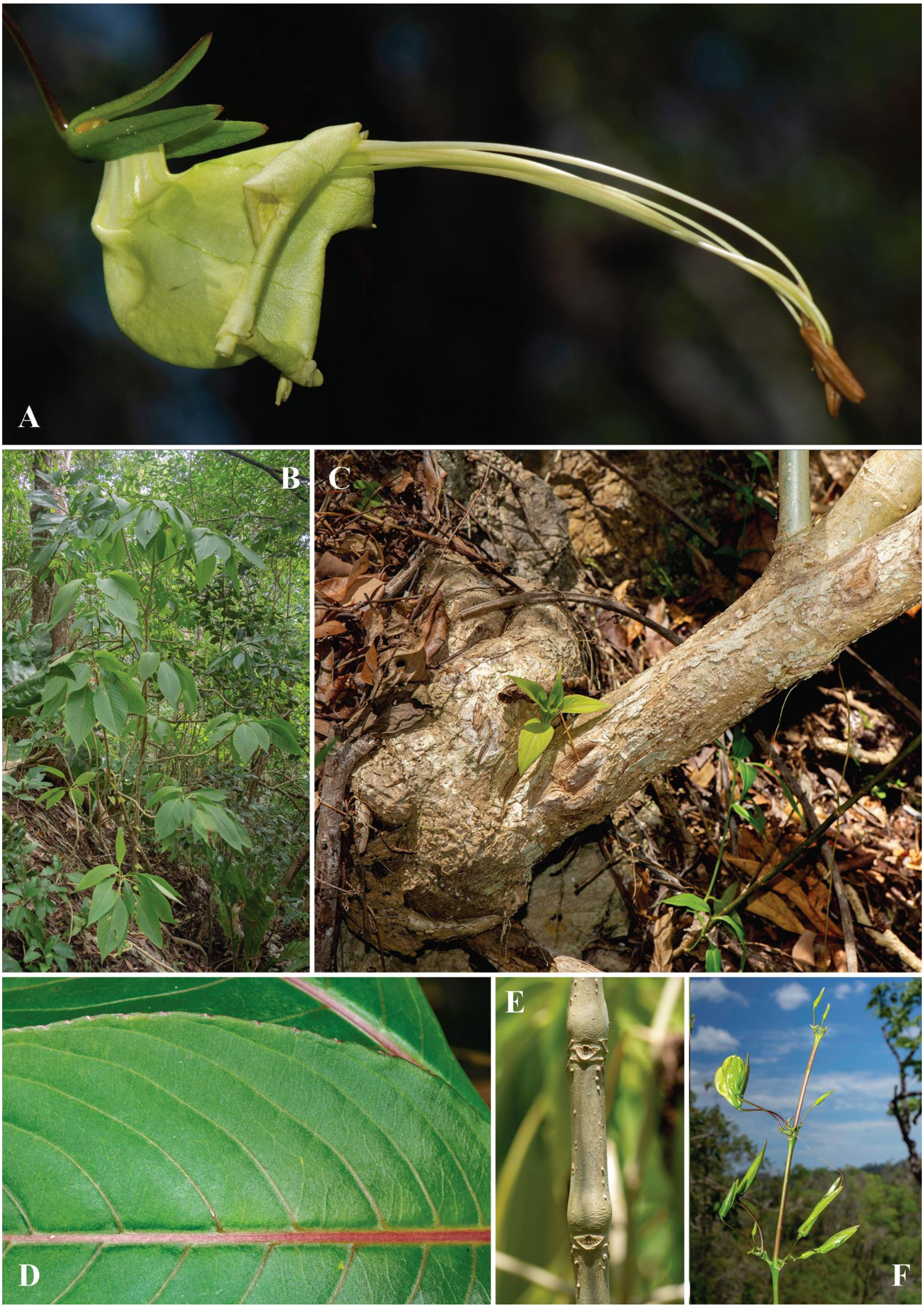
Most calyces have the three lobes that are characteristic of the genus. Five lobes with three prominent lobes and two reduced lobes are evident on *Hinton et al. 15843*; the reduced lobes are 3 to 6 mm long and 0.8 to 2 mm wide. Five-lobed calyces in inflorescences are likely teratological and suggest suppression rather than fusion of lobes for typical plants with three-lobed calyces.

Additional specimens examined.— MEXICO. **Michoacán**: Mpio. Aquila, KM 6.7 carretera Aquila–Coalcomán, 18°36'38"N, 103°28'32"W, *P. Carillo-Reyes & V. Steinmann 5484* (CAS, RSA); between Coalcomán and Aquila, 5.6 km NE of Aquila, 18°36'32.54"N, 103°28'31.38"W, *T. Daniel & V. Steinmann 11913* (CAS, COLO, MEXU, MO, NY, US), cultivated plants of this collection grown from seed in San Francisco, California, *11913cv* (CAS); Aquila [ca. 18°35'49.39"N, 103°30'14.64"W], *G. Hinton et al. 15843* (RSA, US).

2. *Louteridium chartaceum* Leonard, *Publ. Carnegie Inst. Wash.* 461:197. 1936. **Type.**— BELIZE. **Belize**: Gracie Rock, Sibun River [ca. 17°23'13.67"N, 088°27'1.91"W], 24-III-1935 (flr, frt), *P. Gentle 1526* (holotype: US-1589669!; isotypes: A-image seen, ARIZ!, K!, LL!, MICH!, MO!, NY!, US-1589668!, WIS-image seen).

Shrubs to trees to 3.5 m tall, often epipetric. Older (woody) stems irregularly striate, ± lenticellate, lacking trichomes; younger (herbaceous) stems subterete to subquadrate, glabrous. Leaves seasonally deciduous, ± clustered just proximal to inflorescence, petiolate (or distal leaves subsessile), petioles to 70 mm long, blades subsucculent, ovate to elliptic (to obovate-elliptic), 70–285 mm long, 30–95 mm wide, 1.7–3.7 × longer than wide, acuminate to subfalcate at apex, rounded

Figure 12 (right). *Louteridium chartaceum* (*Brewer 7176*). A. Flower. B. Habit of young plant showing clusters of leaves. C. Trunk of mature plant growing on rocky slope. D. Portion of mature leaf showing red to pink veins and marginal swellings/encrustations. E. Older stem showing swelling above nodes, raised lenticels, and leaf scars. F. Inflorescence with lateral short shoots, persistent calyces on old flowers, and a nearly mature floral bud. Photos by S. Brewer (to whom copyrights are reserved), used with permission.


A
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to acute (distal leaves) to attenuate (proximal leaves) at base, surfaces glabrous, margin entire and sometimes with inconspicuous marginal swellings/encrustations. Inflorescence a terminal (raceme to) racemose thyrse to thyrse to 580 mm long (including peduncle and excluding corollas), peduncle to 240 mm long, glabrous, rachis glabrous; dichasia expanded or sometimes modified by very short expansion between pairs of succeeding flowers with the congested dichasial axis becoming a ± linear racemelike lateral short-shoot to 10 mm long, opposite, sessile to pedunculate, (1–) many-flowered, to 70 mm long (excluding corollas), dichasial peduncles (if present) to 24 mm long, glabrous. Bracts caducous, subfoliose, ovate to lanceolate, 18–52 mm long, 3.5–18 mm wide, reduced in size toward apex, abaxially glabrous. Bracteoles caducous, triangular, 2–7 mm long, 1.5–2.5 mm wide, abaxially glabrous. Flowers pedicellate, pedicels 30–43 mm long, glabrous. Calyx 18–26 (–29 in fruit) mm long, lobes fused at base for 1–1.5 mm, subheteromorphic, subsucculent, linear to lance-linear, 15–25 mm long, 3–5 mm wide, (subrounded) to acute at apex, abaxially glandular-punctate (punctations to 0.1 mm in diameter, sometimes sparse) but lacking elongate trichomes, posterior lobe subplanar to subconduplicate, 15–23 mm long, equal to or shorter than lateral lobes, 3–5 mm wide, lateral lobes 17–25 mm long, 3.2–5 mm wide, all lobes (subrounded to) acute at apex. Corolla light green or greenish yellow with lobes usually becoming slightly maroon-tinged and darker maroon at distal tips with age, 35–40 mm long, externally glabrous, tube 21–23 mm long, narrow proximal portion 5–8 mm long, 6–11 mm in diameter near midpoint, throat 14–17 mm long, 19–23 mm in diameter at mouth, lobes recurved to recoiled, oblong to ovate-elliptic, 12–14.5 mm long, 8.5–10.5 mm wide, rounded and bifid at apex. Stamens 4, 55–77 mm long, distally glabrous, pubescent near base with eglandular trichomes, thecae yellowish green, 6.5–9.5 mm long; staminode 1, ± triangular, 0.1–1.5 mm long. Style 60–67 mm long, glabrous, stigma unequally 2-lobed and ± obliquely funnelform, 1.5–2 mm long, lobes ± elliptic, 1–1.5 mm long, 0.6–1 mm wide. Capsule (20–) 23–26 mm long, 4–6 mm in diameter, glabrous, stipe 1.5–2 mm long. Seeds up to 16 per capsule, 4–4.5 mm long, 3–4 mm wide, surfaces with subconic to low rounded protrusions or becoming smooth.

Phenology.— Flowering: January–March; fruiting: February–March, June. In the two populations of this species observed for ca. one hour each, floral buds were present on the plants at both sites during daylight hours (morning for *Daniel 8294* and afternoon for *Daniel & Butterwick 5905*), and mature fallen flowers were present on the ground at one site (*Daniel 8294*). Likewise, *Brewer et al. 7176* notes that the corollas fall in the morning.

Distribution and habitat.— East-central Belize (Belize, Cayo; Fig. 10); plants occur on steep limestone slopes in evergreen seasonal forests (tropical evergreen seasonal broadleaf lowland forest fide Meerman and Sabido 2001) at elevations from 10 to 120 m.

Illustrations.— Figure 12; Leonard (1936:197, fig. 1).

Conservation.— Daniel (1997) noted that the population at the type locality had been destroyed by quarrying activities, but that other populations had been located on several of the small, isolated, and steep limestone hills in the southern portion of the coastal plain in Belize District. *Louteridium chartaceum* has since (i.e., in 2005) been located in Cayo District, as well. Plants occur in at least three protected areas, and the species' EOO (189 km^2) includes a portion of another one. Ecologist and botanist Steven Brewer (in litt., 14 May 2018) indicates that the species "is common though not abundant on ridge-tops and exposed limestone along the north side of the Maya Mountains in Cayo and Belize districts." Brewer (in litt., 22 May 2018) also notes that in this region, potential threats to all of the limestone forests include land conversion via agriculture (both in and around protected areas), encroachment or settlement in protected areas, and fire (either natural or "escaping" flames from regular burning used to clear nearby agricultural fields or bush).

In the same communication, Brewer also observed that, "*L. chartaceum* (though I doubt the same is true for *L. donnell-smithii*) is surprisingly resilient from the effects of even very hot fires. Natural light fires are occasional on those limestone hills and so it seems that most species there are tolerant or resilient in the face of light fires." Scant change in vegetation cover within the EOO is evident from the historical imagery (1969 to 2016) seen via Google Earth Pro (2018). If the three protected areas in which the species occurs are treated either as a single or multiple locations, and the unprotected areas are treated as another location under threat (i.e., conversion of nearby, and partly within the EOO, land to agriculture as an inferred or projected threat), a preliminary conservation assessment of Endangered (EN; B1, a, b) can be proposed for *L. chartaceum*.

Discussion.— Plants grown in San Francisco from cuttings of *Louteridium chartaceum* from the type locality (*Daniel & Butterwick 5905cv*) produced floral buds that attained 35 mm in length but abscised prior to opening. Both thyrses and racemose thyrses are present on *Brewer et al. 7176*. Bracteoles of a pair are sometimes fused basally for about 1 mm, at least along one side.

Additional specimens examined.— BELIZE. **Belize**: Runaway Creek Nature Reserve, E of Coastal Road, 17°18'44"N, 088°27'23"W, *S. Brewer et al. 7176* (MO-image seen); along Coastal Hwy. near milepost 18, ca. 5 km W of Gales Point toward La Democracia, ca. 17°11'N, 088°22'W, *T. Daniel 8294* (BR, CAS, MEXU, MICH, MO, US); Gracie Rock Hill near Rockville Quarry between Western Hwy. and Sibun River, ca. 30 km SW of Belize City [ca. 17°23'13.67"N, 088°27'1.91"W], *T. Daniel & M. Butterwick 5905* (C, CAS, K, MICH, MO, NY), cultivated plants of this collection grown from cuttings in San Francisco, California, *5905cv* (CAS); Gracie Rock, 1.5–4 mi S of Mile 22 on Western Hwy., *J. Dwyer 10959* (LL, MEXU, MO), *R. Liesner & J. Dwyer 1485* (BM, DUKE, MO, NY, TEX). **Cayo**: Manatee Forest Reserve, Banks of Indian Creek, at confluence of Yaha and Indian Creek, 1 km W from Daylight Cave, 17°12'54.2"N, 088°33'19.4"W, *H. Baden & D. Harris 3* (BM).

3. *Louteridium costaricense* Radlk. & Donn. Sm., *Bot. Gaz. (Crawfordsville)* 37:422. 1904. **Type**.— COSTA RICA. **Cartago**: Tucurrique, Las Vueltas [ca. 09°50'53.61"N, 083°43'35.82"W], 1000 m, III-1899 (flr), *A. Tonduz 8123* (holotype: US!).

Perennial herbs to shrubs to 2 m tall, terrestrial. Older (woody) stems subquadrate, lenticellate, lacking trichomes; younger (herbaceous) stems subquadrate to flattened, glabrous. Leaves not all seasonally deciduous, ± evenly distributed along stems, petiolate, petioles to 85 mm long, blades subsucculent, (ovate-elliptic to) elliptic to obovate, 125–335 mm long, 43–153 mm wide, 2.2–3.2 × longer than wide, acute to acuminate to acuminate-falcate at apex, attenuate at base, surfaces glabrous, margin entire to sinuate. Inflorescence a terminal pedunculate (racemose thyrse to) thyrse to 335 mm long (including peduncle and excluding corollas), peduncle to 230 mm long, glabrous, rachis glabrous; dichasia often modified via sympodial expansion and appearing like lateral branches, opposite or alternate, (subsessile to) pedunculate, 1–many-flowered, to 117 mm long (excluding corollas), dichasial peduncles 1–15 mm long, glabrous. Bracts persistent, lance-ovate to ovate to elliptic (or subfoliose proximally), 6–70 mm long, 2–24 mm wide, abaxially glabrous or glandular punctate (but lacking elongate trichomes), sometimes with lenticel-like encrustations as well. Bracteoles persistent, ovate to elliptic, 3.5–11 mm long, 2–6.5 mm wide, abaxial surface like that of bracts, those of a pair sometimes basally fused for ca. 1 mm (at least along one side). Flowers pedicellate, pedicels 6–58 mm long, glabrous or sometimes covered with crystal-like punctations or globules or pubescent with stipitate glandular trichomes (sometimes sparse) 0.1–0.2 mm long. Calyx pale green to white, 23–65 mm long, lobes subheteromorphic to heteromorphic, membranaceous, acute to subacuminate at apex, abaxially glabrous or pubescent (at least near base) with sparse glandular trichomes like those of pedicels and conspicuously or inconspicuously glandular-punctate, punctations < 0.1 mm in diameter, posterior lobe planar or ± conduplicate, oblong-lanceolate to ovate to elliptic, 23–65 mm long, longer than lateral lobes, 10–36 mm wide, lateral lobes lance-ovate to ovate to ovate-cordate to elliptic, 21–52 mm long, 7–27 mm wide. Corolla greenish white to pale yellow, 40–60 mm long, externally pubescent with erect to flexuose glandular (0.1–0.5 mm long) and eglandular (0.1–1 mm long) trichomes, trichomes sometimes very sparse, tube 25–46 mm long, narrow proximal portion 3–17 mm long, 4.5–10 mm in diameter near midpoint, throat 22–43 mm long, 17–23 mm in diameter at mouth, lobes spreading to recoiled, broadly triangular to broadly ovate to subcircular, 8–16 mm long, 6–12 mm wide, rounded to acute and ± emarginate at apex. Stamens 2, 52–57 mm long, filaments glabrous distally, not seen proximally, thecae 9–15 mm long; staminodes (if present) not seen. Style 50–55 mm long, glabrous distally, not seen proximally, stigma subequally to unequally 2-lobed, lobes linear-oblong, 3–5.2 mm long, 1.2–1.5 mm wide. Capsule 27–35 mm long, 6–6.5 mm in diameter, glabrous, stipe 7–12 mm long. Seeds up to 16 per capsule, 4–6.2 mm long, 4–6 mm wide, surfaces smooth to wrinkled.

PHENOLOGY.— Flowering: throughout the year; fruiting: June–March. *Folsom et al. 5464* notes that corollas open in the evening; *González 7918* notes that flowers were closed at 17:00 but opened by 19:00.

DISTRIBUTION AND HABITAT.— Costa Rica (Cartago, Guanacaste, Heredia, Limón, Puntarenas, and San José) and Panama (Bocas del Torro, Chiriquí, Colón, and Guna Yala), primarily (or exclusively?) on the Caribbean versant (Fig. 9); plants occur in and along streams in lowland to montane wet forests and cloud forests at elevations from 15 to 1700 m.

ILLUSTRATIONS.— Figure 4A, B; Durkee (1978:232, fig. 20); Durkee (1985:14, fig. 12).

CONSERVATION.— *Louteridium costaricense* has the largest EOO (61,058 km^2) among congeners. Its EOO includes at least 23 protected areas (16 in Costa Rica and seven in Panama), and the species has been collected in five of them. Although there are undoubtedly threats to the species in various portions of its extensive geographic range, considering its overall distribution and relative abundance, the species is here assessed as Least Concern (LC; IUCN 2017).

DISCUSSION.— Corollas of *Louteridium costaricense* are more tubular and generally less open than in congeners. No significant differences were encountered between plants from Costa Rica and those from Panama. Considerable variation is evident in the shape and width of corolla lobes from oblong-lanceolate to lance-ovate and 7 to 12 mm wide (e.g., *Tonduz 8123*) to ovate-cordate and 21 to 32 mm wide (e.g., *Herrera & Gamboa 8581*).

ADDITIONAL SPECIMENS EXAMINED.— COSTA RICA. **Cartago**: Cantón de Turrialba, Valle del Reventazón, Grano de Oro, El Sies, Moravia de Chirripó, 09°49’50”N, 083°26’40”W, *P. Campos & A. Campos 213* (MO); “Limon, Siquirres, Las Brisas de Pacuarito, camino a Cerro Tigre,” 09°57’00”N, 083°25’50”W [=Cartago Province], *G. Herrera 8840* (K); “Limon, Siquirres, Pacuarito, Las Brisas,” 09°56’10”N, 083°25’20”W [=Cartago Province], *G. Herrera et al. 8646* (K). **Guanacaste**: Cordillera de Tilarán, 1 km N de Las Nubes de Río Chiquito, Zona Monteverde, 10°22’N, 084°51’W, *W. Huber & W. Zuchowski 8681* (MO); “Puntarenas,” Cordillera de Tilarán, Monteverde, San Gerardo Biological Station, Sendero Congo, 1 km W of Station, 10°22’N, 084°48’W [=Guanacaste Province], *D. Penneys 454* (CAS). **Heredia**: Finca La Selva, OTS Field Station on Río Puerto Viejo just E of its jct. with Río Sarapiquí [10°25’53”N, 084°00’13”W], *B. Hammel & J. Trainer 13226* (CAS, DUKE, MO). **Limón**: Cantón Siquirres, Finca de E. Berlin, Pocora, cuenca del Río Destierro, [ca. 10°10’5.11”N, 083°35’41.15”W], *J. González 7918* (LSCR-image seen), *J. González & J. Chaves 8728* (LSCR-image seen), *J. González et al. 8157* (LSCR-image seen); Cantón Siquirres, La Alegría, Alto Botella, [ca. 10°05'45.64"N, 083°36'58.36"W], *J. González et al. 7967* (LSCR-image seen), *9618* (LSCR-image seen); Cantón Siquirres, Florida, Alto Botella, [10°05'19.97"N, 083°33'26.45"W], *J. González et al. 9353* (LSCR-image seen); Cantón Siquirres, Pocora, Cuenca del Río Destierro, Cordillera de Talamanca, Cantón de Matina, 200 m aguas abaja de la confluencia de Quebrada Cañabral con Río Barbilla, 10°00'10"N, 083°25'30"W, *G. Herrera 2286* (DUKE, MO); Almirante, Cerro Chiqui, 09°43'40"N, 083°18'30"W, *G. Herrera & W. Gamboa E. 8581* (F, K, MEXU, MO, NY, US); 10 km SW of Siquirres on road to Turrialba, E of ridge top, *J. MacDougal 1110* (DUKE); Cantón de Limón, Cordillera de Talamanca, Cerro Muchilla, Fila Matama, entrando por pueblo El Progresso, 09°47'40"N, 083°06'30"W, *R. Robles & A. Chacón 2765* (MO). **Puntarenas**: vicinity of Finca Las Cruces, SE of San Vito on road to Via Neilly, [ca. 08°47'14.82"N, 082°57'25.04"W], *R. Weaver et al. 1777* (DUKE). **San José**: from La Montura to Los Chorritos, *L. Gomez et al. 20929* (MO). PANAMA. **Bocas del Torro**: Fish Creek Mts., vicinity of Chiriqui Lagoon [ca. 08°58'59.68"N, 082°13'48.70"W], *H. von Wedel 2283* (MO). **Chiriquí**: Fortuna Dam site [ca. 08°44'46.90"N, 082°14'38.50"W], *J. Folsom & R. Dressler 5464* (MO); La Fortuna hydroelectric project, ridge behind camp, [08°41'25.09"N, 082°13'47.82"W], *B. Hammel 2228* (MEXU, MO). **Colón**: along Río Guanche, 3–7 km above bridge [ca. 09°29'N, 079°38'W], *B. Hammel et al. 4916* (MO); ca. 2–3 mi up Río Guanche [ca. 09°30'30"N, 079°39'30"W], *H. Kennedy & R. Foster 2180* (MO). **Guna Yala** (**San Blas**): Nusagandi, El Llano–Cartí Road, along creek on Atlantic slope [ca. 09°18'18.56"N, 078°59'20.14"W], *G. de Nevers & B. González 3656* (DUKE, MEXU, MO); El Llano–Cartí Road, KM 19.1 [ca. 09°20'51.93"N, 079°01'54.94"W], *G. de Nevers et al. 6195* (CAS, DUKE, MEXU, MO); trail to Cerro Obu (Habu of maps) from Río Urgandi (Río Sidra) [ca. 09°23'59.51"N, 078°49'40.88"W], *G. de Nevers et al. 8007* (CAS, MO); El Llano–Cartí hwy., ca. 23 km N of El Llano, *R. Dressler 4310* (DUKE, ENCB, F, MO); Nusagandi, El Llano–Cartí road, 09°19'N, 078°55'W, *H. van der Werff 7019* (CAS, MO).

4. *Louteridium dendropilosum* T.F. Daniel**,** *Proc. Calif. Acad. Sci.* 64:140. 2017. **Type.**— MEXICO. **Oaxaca**: Distr. Pochutla, Mpio. San Miguel del Puerto, Arroyo Arena, ca. 100 m downstream from jct. Río Laja, ca. 3 km SE of Rancho Dioon toward Xadani, 15°58'51.33"N, 096°05'53.91"W, 600 m, evergreen seasonal forest (selva mediana subperennifolia), 29-III-2011, T. *Daniel, A. Sánchez, and J. Pascual 11784* (holotype: MEXU!; isotypes: CAS! COLO! K! MO! NY! SERO! US!).

Shrubs to trees to 12 m tall, sometimes epipetric. Older (woody) stems quadrate, lenticellate, irregularly striate-sulcate, lacking trichomes; younger (herbaceous) stems subquadrate-sulcate, sparsely lenticellate, irregularly fissured, evenly pubescent with erect to flexuose simple and dendritic (sparse) eglandular trichomes <0.1–0.5 mm long. Leaves seasonally deciduous, ± clustered at apex of old growth or at apex of an otherwise leafless shoot of new growth, petiolate, petioles to 65 mm long, blades subsucculent, ovate to elliptic to broadly elliptic, 76–190 mm long, 40–122 mm wide, 1.4–2.5 × longer than wide, apiculate to acuminate at apex, rounded to acute to attenuate at base, adaxial surface pubescent with simple and dendritic eglandular trichomes, trichomes soon becoming ± restricted to proximal portion or to midvein, abaxial surface pubescent (especially along veins) with dendritic trichomes to 0.5 mm long, midvein often pinkish or reddish, margin entire (sometimes undulate and appearing subcrenate). Inflorescence a terminal subsessile to pedunculate raceme to 220 mm long, peduncle to 50 mm long, pubescent like young stems, rachis pubescent like young stems; dichasia opposite or alternate, sessile, 1-flowered, to 47 mm long (excluding corollas). Bracts caducous, lanceolate to lance-ovate, 11–16 mm long, 2.5–6 mm wide, abaxially pubescent with simple and dendritic trichomes 0.05–0.2 mm long. Bracteoles caducous, lanceolate to lance-elliptic, 7–9 mm long, 2–3 mm wide, abaxially pubescent like bracts. Flowers pedicellate, pedicels 21–46 mm long, pubescent like rachis or with the trichomes to 1 mm long. Calyx 17–32 mm long, lobes fused at base for 1–1.5 mm, subhomomorphic to subheteromorphic, membranaceous, subelliptic to ovate-elliptic to subrhombic-obovate, rounded to acute at apex, abaxially pubescent with mostly dendritic trichomes 0.1–0.5 mm long, posterior lobe planar, 17–32 mm long, 10–19 mm wide, usually slightly larger and sometimes more conspicuously venose than lateral lobes, major veins often maroon, lateral lobes 20–31 mm long, 8–18 mm wide. Corolla light green or greenish yellow, sometimes with maroon on limb (especially at base of lobes) and distal portion of throat, externally glabrous (inconspicuously glandular punctate but lacking elongate trichomes), 50–62 mm long, tube 35–37 mm long, narrow proximal portion 11–15 mm long, 6–10.5 mm diameter near midpoint, throat 20–24 mm long, 25–35 mm diameter at mouth, lobes recurved to recoiled, broadly ovate to subtriangular, 13–20 mm long, 10–21 mm wide, entire at apex. Stamens 4, 60–80 mm long, filaments glabrous distally, glabrous or pubescent with eglandular trichomes near base, thecae 8–10.5 mm long; staminode 1, rodlike, 0.6–40 mm long. Style 70–101 mm long, distally glabrous, pubescent with eglandular and glandular trichomes near base, stigma equally 2-lobed, lobes broadly elliptic to broadly ovate-triangular, 1–2 mm long, 1–1.4 mm wide. Capsule 21–28 mm long, 6.5–9.5 mm in diameter, densely pubescent with erect glandular trichomes 0.05–0.5 mm long and with an overstory (sometimes sparse) of erect to flexuose (sometimes dendritic) eglandular trichomes to 1.4 mm long, stipe 2.5–3.5 mm long. Seeds up to 16 per capsule, 5.2–7 mm long, 5–6.4 mm wide, surfaces smooth.

PHENOLOGY.— Flowering: February–March; fruiting: March–April. Based on field observations and cultivated plants (*Daniel et al. 11894cv*), flowering occurs on leafless (or nearly leafless) plants during the dry season. Near the end of the dry season (e.g., late March–April) when flowering is waning and fruits are mature, a new flush of vegetative growth appears from axils of clustered leaf scars at the base of the inflorescence, which eventually falls away. New internodal stem elongation (e.g., the young stems of the description above) takes place from the axil of a leaf scar on the old growth and terminates in a cluster of new leaves and/or between at least one of the pairs of leaves in the cluster and the remaining cluster.

Field observations of *Daniel et al. 11894* over three days (24–26 February 2012) revealed: day 1 between 08:00–09:00 (light) — corollas mostly fallen, only a few from previous night still attached to tree; day 2 between 19:00–20:00 (dark) — all corollas open, ca. 100 seen, bats active around plants but none seen visiting flowers, no floral odor detected and no nectar visible in saccate tube of undissected corollas, stigma extended ca. 1 cm beyond anthers on fresh flowers, stigma of 7 flowers examined for pollen (all pollinated); day 3 between 17:30–18:30 (light) — many corollas open and many others still in bud, corollas open fully (including recurving of corolla lobes) in 15 to 20 seconds, open flowers actively visited by Cinnamon Hummingbird (*Amazilia rutila*, species det. by Jeff Chemnick), birds probe for nectar once or twice at same flower before moving on, nectar is located behind a barrier (seen in dissected flowers) at the base of the tube, nectar not visible in the saccate throat, birds appear to contact anthers with head or back and presumably contact the stigma on some visits as well, birds visit between 5–10 flowers on a single plant or on multiple plants before moving away from an area or resting on a branch, 2 flowers were observed to open and when subsequently visited by a hummingbird (one flower visited once, other flower visited twice) they were checked for pollination (no pollen observed on stigma of either), small bees or flies also observed visiting flowers but they only contact anthers, buds continue opening until full darkness (at 18:30); day 3 between 18:30–20:30 (dark) — hummingbirds no longer active, bats very active around plants but none observed visiting flowers.

On a single flower of *Daniel et al. 11894cv* grown in San Francisco, corolla lobes began to separate at 15:50 and the corolla was fully open (lobes spreading 90° with respect to the throat or reflexed) with the stamens and style fully exserted by 16:15. By 18:00, all corolla lobes were at least partially recoiled. At 23:00, 6.5 µl of nectar was encountered in the nectar chamber, and the stigma was dusted with pollen from the anthers. At 07:15 the next day, 72.1 µl of nectar was recovered from the nectar chamber. The corolla abscised and fell from the persisting flower at 07:45. Thus, the corolla of the pollinated flower persisted for ca. 16 hours.

Distribution and habitat.— Southern Mexico (Oaxaca; Fig. 8) in the Sierra Madre del Sur and the Isthmus of Tehuantepec; plants occur on limestone (often karstic) slopes of streams in tropical deciduous forests and tropical subdeciduous forests at elevations from 600 to 750 m.

Illustrations.— Figure 2F–L; Daniel (2017:143, fig. 8).

Conservation.— A discussion and preliminary conservation assessment of Endangered (En) was proposed for this species (B1, a, b; IUCN 2017) by Daniel (2017).

Discussion.— *Louteridium dendropilosum* is unique among congeners by its dendritic trichomes, which are present on both vegetative and reproductive organs. Trichomes of other species may consist of one or more cells and be either glandular or eglandular, but they are not branched. Bracts and bracteoles are caducous prior to maturation of the flowers associated with them; thus, they are rarely encountered and are not present on any of the wild-collected specimens. The data on their shape, size, and pubescence noted above were taken just prior to their dehiscence from the young inflorescence of a cultivated plant (*Daniel et al. 11894cv*).

Additional specimens examined.— MEXICO. **Oaxaca**: Distr. Pochutla, Mpio. San Miguel del Puerto, Arroyo Arena, ca. 100 m downstream from jct. Río Laja, ca. 3 km SE of Rancho Dioon toward Xadani, 15°58'51.33"N, 096° 05'53.91"W, *T. Daniel, et al. 11894* (CAS, MEXU), *12187* (CAS, MEXU), cultivated plants of *11894* grown from seeds in San Francisco, California, *11894cv* (CAS); Mpio. El Barrio, 9 km N [sic] de El Barrio, Cerro Palmasola, antena microondas [ca. 16°44'32.52"N, 095°05'36.04"W], *R. Fernández N. 4189* (IEB, NY); Distr. Pochutla, Mpio. San Miguel del Puerto, Arroyo Arena, 15°58'39.7"N, 096°05'54.9"W, *J. Pascual 1396* (MEXU, SERO, TEX); Distr. Pochutla, Mpio. San Miguel del Puerto, 300 m de la terracería sobre la vereda rumbo Río la Laja, 15°58'49.9"N, 096°06'6.9"W, *A. Saynes V. et al. 3831* (MEXU, SERO); Distr. Juchitán, Mpio. El Barrio, parte alta del Cerro Palmasola, junto a la antena de microondas [ca. 16°44'32.52"N, 095°5'36.04"W], *S. Zamudio R. 6352* (CAS, IEB).

5. *Louteridium donnell-smithii* S. Watson, *Proc. Amer. Acad. Arts* 23:284. 1888. **Type**.— GUATEMALA. **Alta Verapaz**: Pansamalá, 3800 ft., V-1887 (flr, frt), *H. von Türckheim 856* (holotype: GH-00094124-images seen; see discussion).

Shrubs or trees to 12 m tall, terrestrial or epipetric. Older (woody) stems subquadrate to quadrate, irregularly striate-fissured, pubescent or glabrate; younger (herbaceous) stems quadrate to quadrate-sulcate, densely pubescent with erect to flexuose eglandular trichomes to 2 mm long (distal 1 or several internodes sometimes with glandular trichomes as well). Leaves not all seasonally deciduous, evenly distributed on young shoots, petiolate, petioles to 190 mm long, blades membranaceous, ovate to broadly ovate to cordate, 140–465 mm long, 85–316 mm wide, 1–2 × longer than wide, acuminate at apex, acute to rounded to cordate at base, surfaces densely pubescent with cauline type trichomes, margin crenate-dentate with rounded (to acute) teeth up to 2 mm long. Inflorescence a terminal pedunculate raceme to thyrse to 450 mm long (including peduncles and excluding corollas), peduncle to 250 mm long, pubescent with flexuose glandular and eglandular trichomes to 2.8 mm long (viscid), rachis viscid; dichasia opposite, sessile or pedunculate, (1–) 3–5 (–many)-flowered, to 130 (–185) mm long (excluding corollas), dichasial peduncles to

5 (to 35 or to 90 at proximal nodes) mm long, viscid. Bracts foliose to subfoliose and often persistent proximally, reduced in size and caducous (usually only scars present) distally, proximalmost pair sessile to subsessile, lanceolate to cordate, similar to leaves except smaller (e.g., 45 × 32 mm), distal pairs ovate to lanceolate, 10–22 mm long, 2.5–9 mm wide, abaxially pubescent like leaves (i.e., trichomes mostly eglandular). Bracteoles and secondary bracteoles usually present on young inflorescences but becoming deciduous as inflorescence matures, linear to lanceolate, 3.5–13 mm long, 1–3.4 mm wide, abaxially pubescent like bracts or viscid. Flowers pedicellate, pedicels to 105 mm long, viscid with trichomes mostly glandular. Calyx 22–35 (–40 in fruit) mm long, lobes fused at base for 1–3 mm, heteromorphic, membranaceous, abaxially viscid where exposed in bud, posterior lobe conduplicate, ovate, 21–37 mm long, equaling to longer than lateral lobes, 8–15 mm wide, acuminate to subfalcate at apex, lateral lobes lunate, 17–33 (–37) mm long, 6–10.5 mm wide, acute to subacuminate at apex. Corolla cream to green-yellow with maroon veins to pale maroon, 41–57 mm long, externally viscid or pubescent (sometimes sparsely so) with erect to flexuose glandular trichomes 0.05–0.3 mm long, tube 25–34 mm long, narrow proximal portion 8–14 mm long, 5.7–9 mm in diameter near midpoint, throat 15–24 mm long, 25–38 mm in diameter at mouth, lobes recoiled, broadly ovate to subtriangular, 16–20 mm long, 13–15 mm wide, acute or emarginate at apex. Stamens 2, 65–85 mm long, filaments glabrous distally, pubescent proximally with eglandular trichomes, thecae 10–15 mm long; staminodes 2, 0.5 mm long. Style 76–85 mm long, glabrous (or with a few glandular trichomes near base), stigma subequally to unequally 2-lobed and often ± funnelform, lobes broadly elliptic to obovate to 3-pronged, 1–2.2 mm long, 0.7–2.1 mm wide. Capsule 21–31 mm long, 5–8 mm in diameter, pubescent with erect glandular trichomes 0.1–0.8 mm long, stipe 1.5–2.5 mm long. Seeds 12–16 per capsule, 4.5–5.5 mm long, 4–5 mm wide, surfaces minutely papillose in longitudinal rows.

PHENOLOGY.— Flowering: November–June; fruiting: December–June. *Brewer et al. 5748* notes corollas opening at night, just after dark. *Davidse & Brant 32089* and *Gregory 612* note corollas opening at dusk or in the evening and withering by sunrise. Daniel (2010) noted floral color forms with different flowering times (see below). Fredy Archila (in litt. January 2012) observed both bats and moths visiting flowers of *L. donnell-smithii* in and around Cobán, Guatemala over a period of years.

DISTRIBUTION AND HABITAT.— Southern Mexico (Chiapas), Belize, Guatemala, Honduras (Fig. 10); plants occur, usually on limestone (often karstic), on slopes and along streams in lowland moist to wet forests, mesophytic montane forests, montane rain forests, and cloud forests at elevations from 1 to 1600 (to 2100) meters.

ILLUSTRATIONS.— Figures 13, 4C, D; Lindau (1895:294, fig. 118); Gibson (1974:407, fig. 90).

LOCAL NAMES.— “Carreton” (*Lentz et al. 2428*), “matacucuyuchi” (*Miranda 7163*); “oxox če” (*Williams & Wilson 40437* and *Wilson 40943*, Quecchí name); “palpalte” (*Ochoa 80*); “tabaco silvestre” (*Contreras 5510*); “vejiga” (*Standley 91236*); “ulul k’uum” (*Ventur 177*).

USES.— *Williams & Wilson 40437* notes that the young growth is eaten; *Ochoa 80* indicates that “esta planta es comida por el jabali.”

CONSERVATION.— *Louteridium donnell-smithii* is the most commonly collected species of the genus, and it is also infrequently cultivated in botanical gardens. Its EOO (32,499 km^2) encompasses all or parts of at least 40 protected areas (10 in Belize, 19 in Guatemala, 9 in Honduras, two in Mexico). Collections of the species have been made in 13 of these areas. The species has been abundantly collected in most portions of its EOO, and in some regions it was sometimes noted on collection labels or observed (TFD) to be common. Fredy Archila of Cobán, Guatemala indicates (in litt. Jan 2012) that in the vicinity of Cobán there were hundreds of trees of *L. donnell-smithii* in

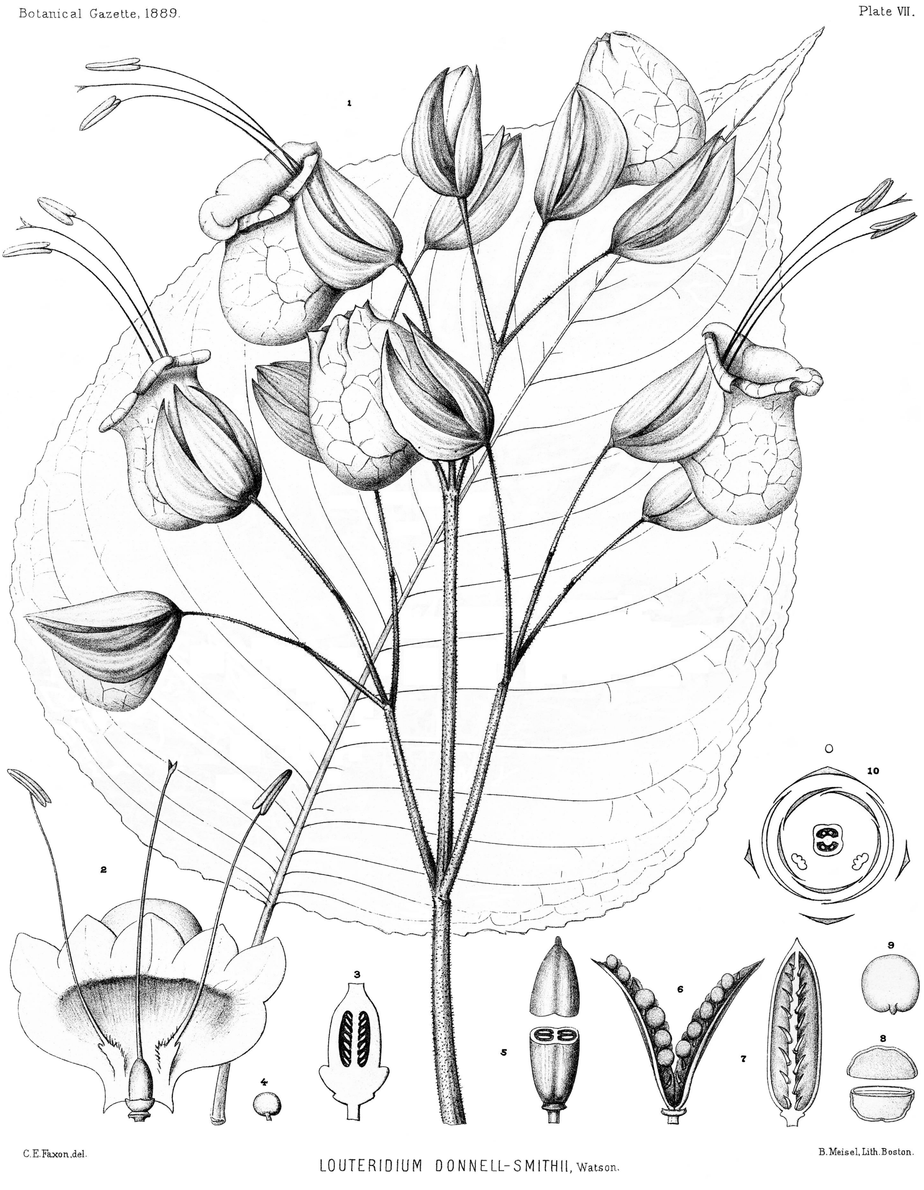

FIGURE 13. *Louteridium donnell-smithii*. Plate 7 from *Botanical Gazette*, vol. 14 (1889), drawn by C.E. Faxon. From the legend on page 29 of Donnell-Smith's article, "Undescribed plants from Guatemala. V:" "Fig. 1. Cyme and leaf. Fig. 2. Flower with calyx removed and corolla laid open. Fig. 3. Vertical section of ovary. Fig. 4. Ovule. Fig. 5. Capsule divided transversely. Fig. 6. Dehiscent capsule. Fig. 7. One valve showing placenta and retinacula. Fig. 8. Seed divided transversely. Fig. 9 Embryo. Fig. 10. Diagram of flower."

the 1980s. Although most of these are no longer extant, some still remain as street trees in that city. Based on these data, this species is accorded a preliminary conservation assessment of Least Concern (LC).

Discussion.— In the protologue, Watson (1888) provided the collection information cited above. The holotype has been cited by various authors (e.g., Richardson 1972; Daniel 1995) as being at US. Indeed, a specimen there (accession: 1320518 with image number: 00136468) was annotated by D. Gibson and T. Daniel as the holotype. This somewhat fragmentary specimen, originally in H. Rusby's herbarium, bears von Türckheim's number 856 (as indicated in the protologue), but notes a collection date of February 1886. The date of collection of the specimen from Pansamalá indicated in the protologue is May 1887. The specimen at GH, where Watson conducted his studies, bears the date noted in the protologue and an annotation written by Watson stating, "Louteridium Donnell-Smithii, Watson-n. gen." Therefore the specimen at GH indicated above conforms to the information in the protologue. The earlier annotations by Gibson and Daniel of the specimen at US are considered to be erroneous, and the specimen at GH noted above is treated as the holotype. This flowering and fruiting specimen lacks leaves, which are described in the protologue. However, drawings of the leaves are on another sheet at GH bearing the same barcode number. If the drawings are original material, the holotype would be considered as mounted on two sheets, and if they were made subsequently, the sheet with an inflorescence, flowers, and fruits would be considered as the holotype. Other collections that bear von Türckheim's number 856, but with a date of February 1886, are located at the following herbaria: K, NY, P, PH, US (although one of three specimens at US has both "1887" and February 1886 on it). Whether these represent isotypes with an incorrect date (i.e., actually collected in May 1887) or the same collection number was used for gatherings of this species during different visits to Pansamalá on various dates remains unknown.

Daniel (2010) noted variation in the timing of anthesis, color of corollas, and diurnal visitation to dark-colored flowers by hummingbirds in this species. There is a possible correlation with cream to green-yellow corollas at lower elevations and chestnut to maroon corollas at higher elevations. Based on specimens of *L. donnell-smithii* at F, which are mostly from Guatemala, plants with cream to green-yellow corollas occur from 75 to 630 m, whereas those with chestnut to maroon corollas occur at 1000 to 2100 m. Figures 4C and D show these extremes of corolla coloration in Guatemala. Other flowers show various degrees of maroon coloration on cream-yellowish corollas. Based on a larger sample of herbarium specimens that include data on corolla color and elevation, it would appear that both the cream to green-yellow and chestnut to maroon color forms occur in Chiapas, Belize, and Guatemala, but that there is no clear difference in elevational ranges of these forms in Chiapas and Belize. However, it is somewhat difficult to correlate corolla color and elevation from herbarium specimens because of variation in the terminology of colors used by collectors. Additional studies that address the different (or at least partially so) flowering times of the different color forms and their primary pollinators, as well as any correlation of floral color with elevation, are desirable.

The inflorescence of *L. donnell-smithii* is commonly a somewhat contracted thyrse at the proximal nodes (with dichasial peduncles usually to 5 mm long) and a raceme (with sessile dichasia) distally. Several collections (e.g., *Armour & Chable 6047*, *Hawkins 981*, *Vargas et al. 1183*) have exceptionally elongate peduncles (to 90 mm long) with expanded dichasia (e.g., secondary peduncles to 55 mm long). These latter dichasia are usually only at the proximal 1 to 3 nodes.

Additional specimens examined.— MEXICO. **Chiapas**: Las Nubes, *F. Billiet 8889* (BR); Mpio. Ocosingo, W end of Laguna Ocotal Grande, [ca. 16°50'26.15"N, 091°28'5.95"W], *D. Breedlove 15709* (DS, F, LL, MICH, NY, US); Mpio. Las Margaritas, western side of Laguna

Miramar E of San Quintín, [ca. 16°24’24.45”N, 091°18’6.60”W], *D. Breedlove 33282* (DS, ENCB, F, LL, MEXU, MICH); Mpio. La Independencia, valley of Santa Elena along rd. to Ixcán, 30 km E of paved rd. at Montebello, [ca. 16°15’57.16”N, 091°49’20.79”W], *D. Breedlove 41991* (DS, MO); Mpio. La Trinitaria, 10 km ENE of Dos Lagos above Sta. Elena, *D. Breedlove 49721* (CAS, ENCB), *D. Breedlove & F. Almeda 57578* (CAS, ENCB, NY); Mpio. Ocosingo, near lake at Naja, [ca. 16°59’4.48”N, 091°35’11.70”W], *D. Breedlove 49962* (CAS, MEXU); Mpio. Ocosingo, 70 km SW of Palenque on rd. to Ocosingo along the Jol Uk’um, [ca. 17°10’33.18”N, 092°06’54.71”W], *D. Breedlove 50875* (CAS, ENCB), *D. Breedlove & F. Almeda 48259* (CAS); Mpio. La Trinitaria, KM 21–23 along road from Lago Tzizcao toward Santa Elena, [ca. 16°06’20.94”N, 091°34’48.32”W], *D. Breedlove & M. Bourell 68070* (BR, CAS, MEXU, US), *D. Breedlove & T. Daniel 71197* (CAS); Mpio. Ocosingo, 1 km S de Naja, camino a Monte Líbano, [ca. 16°58’25.71”N, 091°35’15.33”W], *E. Martínez 17416* (MEXU, MO); Mpio. Ocosingo, Naha, 15 km N de Monte Líbano, camino a Chancala, *E. Martínez S. 18025* (MEXU); Mpio. Ocosingo, Cañón del Colorado, *E. Martinez S. & C. Ramos 26235* (K, MEXU, XAL); Mpio. Las Margaritas, 1 km S de Flor del Río, *E. Martínez S. et al. 24768* (B); Mpio. La Trinitaria, KM 18, Col. Cuauhtémoc, [16°05’16.55”N, 092°02’57.11”W], *A. Méndez G. [=A. Ton] 8026* (MEXU); Mpio. Trinitaria, Col. Cuauhtémoc, KM 20 a Montaña Alta, *A. Méndez G. [=A. Ton] 8893* (IEB, MEXU, MO, RSA, XAL); Monte Líbano, 60 km E de Ocosingo, [ca. 16°54’7.71”N, 091°37’10.27”W], *F. Miranda 7163* (MEXU); Mpio. Las Margaritas [= Mpio. Palenque?], NW del ejido José Castillo T., [ca. 17°24’59.51”N, 091°50’10.35”W], *M. Ochoa 80* (MEXU); Mpio. La Independencia, Col. Fco. Madero, ca. de la carretera, [ca. 16°17’23.49”N, 091°54’38.13”W], *T. Ramamoorthy et al. 1930* (CAS, MEXU); near jct. of Río Perlas and Río Jataté at San Quintín and near Laguna Miramar, [ca. 16°23’27.68”N, 091°20’21.96”W], *E. Sohns 1684* (MICH, NY, UC, US); Km. 36–38 al E Tziscao o a 7–9 km al E de Amparo Agua Tinta, sobre el camino Montebello a Bonampak, [ca. 16°07’19.90”N, 091°26’36.06”W], *O. Téllez & J. Villaseñor 6642* (CAS, ENCB, MEXU); Mpio. Ocosingo, 3 km W de Plan de Ayutla, [ca. 16°47’59.90”N, 091°18’58.16”W], *F. Vázquez B. & S. Avandano R. 1650* (ENCB, MEXU, XAL); Mpio. La Trinitaria, ca. 56 km E of La Trinitaria, 9.4 km E of Lago Tziscao, 16°06’N, 091°35’W, *T. Wendt et al. 2409* (CAS, MEXU, MO, TEX). BELIZE. **Cayo**: Maya Mts., central Bladen Nature Reserve, 16°29’41”N, 088°54’43”W, *S. Brewer et al. 5748* (MO); 2.5 mi past Guacamallo Bridge, road to Millionario [16°50’05”N 089°02’12”W], *J. Dwyer & R. Liesner 12313* (BM, DUKE, MEXU, MO, NY); S of San Luis and E of Camp Six [16°54’35”N 089°00’22”W], *J. Dwyer et al. 360* (MEXU, MO); vicinity of Grano de Oro lumber camp, 6 mi S of Millionario [16°40’22”N 089°01’35”W], *A. Gentry 7791* (MO); Central Maya Mts., Macal river, vicinity of Guacamollo Bridge, 16°55’N, 088°55’W, *R. Glaholt 11* (MO); Las Cuevas Research Station to Monkey Tail River, 16°44’N, 088°59’W, *D. Harris 7888* (BM, MO); between San Antonio and Santa Helena, 17°06.290’N, 089°03.457’W, *D. Lentz et al. 2428* (NY); Ceibo Chico, drill site, 16°31’21”N, 089°07’04”W, *M. Peña et al. 947* (MO); Grano de Oro Camp, *M. Peña-Chocarro et al. 1435* (BM, MO); Chiquibul Forest Reserve, 2.2 mi SE of Holtec Camp, *G. Proctor 30106* (BM, LL); 3 km S de New Maria camp, *T. Ramamoorthy et al. 2965* (MEXU); between Las Cuevas and Río Ceibo Chico, 16°43’02”N, 088°59’02”W, *R. Rees et al. 2* (BM, MEXU, MO); Puente Natural, *C. Whitefoord 9125* (BM, MO); Chiquibul Forest Reserve, Natural Arch, *C. Whitefoord 10044* (BM, US); Chiquibul Forest Reserve, Monkey Tail Branch, *C. Whitefoord 10051* (BM); Chiquibul Forest Reserve, road from Caracol junction to New Maria Camp, *C. Whitefoord 10136* (BM, US). **Toledo**: river trail from Blue Creek village to Blue Creek’s source (ca. 1 km N of village), ca. 26 km NW of Punta Gorda, [ca. 16°12’13.03”N, 089°02’49.12”W], *T. Daniel & M. Butterwick 5891* (CAS); Maya Mts. foothills, Solomon Camp, vicinity of jct. Richardson Creek and Bladen Branch, 16°32–33’N, 088°45–46’W, *G. Davidse &*

A. Brant 32089 (CAS, MEXU, MO, US), Maya Mts., canyon along Bladen Branch, from Richardson Creek to Quebrada de Oro, 16°31–33'N, 088°46–49'W, *G. Davidse & A. Brant 32300* (CAS, MO); southern Maya Mts., Bladen Nature Reserve, upper Bladen Branch, 16°29'31"N, 088°54'37"W, *G. Davidse & M. Meadows 35742* (CAS, MO); southern Maya Mts., Bladen Nature Reserve, just S of Upper Bladen Branch and 1.3 km (air) SE of "AC Camp," 16°28'17"N, 088°55'04"W, *G. Davidse et al. 35881* (MO); Mira-Mar Hill, Edwards Road beyond Columbia [ca. 16°19'06"N 089°06'57"W], *P. Gentle 6355* (F, K, LL, MO, UC, US); Camp 1, 3–4 km SE of Union Camp, 16°22'58"N, 089°07'10"W, *T. Hawkins 1387* (CAS); NE side of Blue Creek, upstream from village of Blue Creek, 16°14'N, 089°00'W, *S. Hill 20270* (MO, NLU, NY, US); SW Maya Mts., Columbia River Forest Reserve, Union Camp, 16°23'N, 089°09'W, *B. Holst 4045* (CAS, MO, MEXU); without locale, *Peck 780* (K, GH, NY); Columbia Forest Reserve, vicinity of forest camp, ca. 6 mi S of Cabro, in upper Rio Grande drainage area [ca. 16°19'N 089°03'W], *G. Proctor 36148* (MO); Fern Hill [ca. 5 miles from Punta Gorda fide Lowden 1970:850], *W. Schipp 1110* (BM, F, G, K, MICH, MO, NY, UC).

GUATEMALA. **Alta Verapaz**: antes de Campur, carretera a Cahabón, [ca. 15°35'19.06"N, 090° 02'46.43"W], *J. Castillo Mont 1197* (NY); near Finca Sepacuite, *O. Cook & R. Griggs 205* (US); planted along street in Cobán, 15°28.517'N, 090°22.349'W, 1230 m, *T. Daniel et al. 11335* (CAS, COLO, NY); Sierra de Chamá, along hwy. from Cobán to Chisec, N of Cobán, off of hwy. ca. 1.5 km N of Río Sachichá along rural road, 15°36.019'N, 090°23.333'W, *T. Daniel & M. Véliz 11337* (BIGU, CAS, MO, US); Sierra de Chamá, ca. 2 km above Aldea Sehubub (= 7 km from Chiquixji; = 35 km NE of Cobán), 15°35.928'N, 090°17.559'W to 15°36.842'N, 090°17.955'W, *T. Daniel et al. 11356* (BR, CAS, F, K, MO, NY); Chucaneb, *J. Donnell-Smith 1620* (US); Pansamalá, *J. Donnell-Smith 1621* (G, K, US); Sepacuite, *G. Goll 155* (US); Sebol, [ca. 15°47'7.25"N, 089°56'14.34"W], *C. Lundell 18310* (CAS, F, K, LL, MO, PH, US)**;** road to Finca Trece Aguas, ca. 1.1 mi N of church in Senahú, [ca. 15°25'01.41"N, 089°49'14.17"W], *J. Luteyn & F. Almeda 3516* (DUKE, F); trail between Sepacuité and Secanquim, [ca. 15°26'41.71"N, 089°44'45.44"W], *W. Maxon & R. Hay 3282* (K, NY, US); near Senahú, *W. Maxon & R. Hay 3296* (NY, US); NO de Tactic, 6 km a Estor, *A. Molina R. & A.R. Molina 12303* (F); between Sepacuité and Secanquim, *H. Pittier 320* (NY, US); Tactic, [ca. 15°19'44.02"N, 090°21'6.69"W], *P. Standley 71094* (F); E of Tactic on road to Tamahú, [ca. 15°18'47.45"N, 090°18'26.68"W], *P. Standley 71249* (F), *71342* (F); along Río Frio, S of Santa Cruz, *P. Standley 90192* (F); between Tatic and divide, on road to Tamahú, *P. Standley 90593* (F, US); vicinity of Cobán, [ca. 15°27'53.66"N, 090°21'2.74"W], *P. Standley 91236* (F); between Cobán and Chimoté, near Rubeltein, *J. Steyermark 44171* (US); Pansamalá, *H. von Tuerckheim 856* (NY, US); Cobán, *H. von Tuerckheim II-2033* (NY, US); Cubilquitz, [ca. 15°39'56.02"N, 090°25'38.84"W], *H. von Tuerckheim 7936* (K, MO, NY, US); Senahu, Finca Aguas, [ca. 15°24'53.59"N, 089°48'39.16"W], *M. Véliz 95.4359* (BIGU, MEXU, MO); near San Juan Chamelco, ca. 15°26'N, 090°16'W, *L. Williams & M. Wilson 40437* (F, MEXU); near "La Presa" ca. 6–8 km SE of Cobán, [ca. 15°28'N, 090°19'W], *L. Williams et al. 40323* (F); 1–8 km NW of Cobán, [ca. 15°28'53.47"N, 090°22'55.17"W], *L. Williams et al. 42031* (BM, F, MO, NY); vicinity of San Juan Chamelco, *L. Williams et al. 43189* (F, US); Finca Tres Aguas, *C. Wilson 180* (F); vicinity of San Juan Chamelco, [ca. 15°25'52.07"N, 090°20'10.64"W], *M. Wilson 40943* (F). **Baja Verapaz**: bei Parula [Purulhá], [ca. 15°13'52.37"N, 090°13'27.20"W], *F. Lehmann 1430* (BM); along Río Frio near San Julían [possibly in Alta Verapaz], *L. Williams et al. 43563* (F, MICH). **El Progresso**: near Finca Caieta, [ca. 14°59'00.03"N, 089°53'59.98"W], *J. Steyermark 43768* (F, MICH, US). **Huehuetenango**: Barillas, Aldea San José Maxbal, trail to Laguna Maxbal, 15°58'N, 091°18'W, *M. Christenhusz et al. 5488* (MO); San José Nueva Frontera–Yolnajab, camino hacia Laguna Yolnajab, Nenton, 16°03'30"N, 091°32'47"W, *J. Morales & M. García 4377* (MO); Cerro Chiblac, between Finca San Rafael and Ixcán, Sierra de los Cuchumatanes [ca. 15°46’25”N, 091°13’58”W], *J. Steyermark 49180* (F, US). **Izabal**: 25 km SSW of Puerto Barrios, [ca. 15°34’21.26”N, 088°37’0.05”W], *D. Gregory 612* (CAS, F, US); Modesto Méndez, [ca. 15°53’29.49”N, 089°13’46.15”W], *W. Harmon & J. Fuentes 2089* (MO); Biotopo Chocón Machacas, Livingston, 15°45’56”N, 088°55’55”W, *J. Morales 1959* (MO); Río Dulce, 2–4 mi W of Livingston, [ca, 15°48’12.69”N, 088°46’37.09”W], *J. Steyermark 39562* (F); Chocón River, *S. Watson 292* (US). **Petén**: Dolores, S of village, [ca. 16°30’51.17”N, 089°24’56.87”W], *E. Contreras 2097* (LL, MO, US); N of Lake Macanché, foot of Cerro Rocoso at Mancanché [ca. 16°58’04”N 089°38’20”W], *E. Contreras 5510* (BM, F, K, MO, NY, WIS, US); La Cumbre, W of KM 145, [ca. 16°04’51.97”N, 089°21’3.37”W], *E. Contreras 6646* (F, LL, MO, PH, US); Tikal District, ruins, Naranjo, *O. Cook & R. Martin 79* (US); along Río Dulce–Flores highway near KM 327, ca. 10 km NW of San Pedro Cadenas, 15°58’08.6”N, 089°16’42.7”W, T. *Daniel & M. Véliz 11255* (BIGU, CAS, MICH, US); Strasse von Flores zur Río Dulce-Brücke, Strecke zwischen Poptún und San Luis, 12 km S von Poptún, *H. Kurz & R. Frisch 147* (W), *148* (W); Sayab, Fallabón–Yaxha road, [ca. 17°04’01.49”N, 089°22’56.17”W], *C. Lundell 2081* (F, MICH); Arroyo Dolores, ca. 200 m de Dolores, *R. Ortíz 1569* (F, MO, NY, US); San Luis, [ca. 16°11’37.30”N, 089°25’48.59”W], *P. Ventura 177* (F). **Zacapa**: Volcán de Monos, [ca. 15°08’58.95”N, 089°30’18.66”W], *J. Steyermark 42400* (F, US). Department undetermined: eastern portions of Vera Paz and Chiquimula, *S. Watson s.n.* (K). HONDURAS. **Comayagua**: Villa de Taulabé, Quebrada la Caliche, [ca. 14°39’56.69”N, 087°59’26.20”W], *C. Alduvín 101* (MO); Siguatepeque, [ca. 14°36’10.86”N, 087°47’54.39”W], *J. Edwards P-589* (F); Quebrada el Caliche, SE de la Villa Taulabé, [ca. 14°41’02.38”N, 087°57’02.73”W], *D. Ruiz 138* (NY, TEFH); near Taulabé, *P. Standley et al. 7001* (F); Pito Solo, Lago Yojoa, [ca. 14°47’39.06”N, 087°58’38.47”W], *J. Valerio R. 2940* (F); near Pito Solo, *L. Williams & A. Molina R. 12335* (F); along Lake Yojoa, near Pito Solo, *L. Williams & A. Molina R. 17730* (F). **Copán**: Montaña Los Zapotes, W of Los Zapotes, 18 km N of Copán Ruinas on road to Agua Caliente and 2–3 km W of Los Zapotes school, [ca. 14°59’13.83”N, 089°09’04.57”W], *T. Hawkins 981* (CAS, MO); Montaña Espiritu Santo, 15°05’N, 088°55’W, *T. Hawkins & D. Mejía 185* (EAP, MO). **Cortés**: entre Pito Solo y Agua Azul, Lago Yojoa, [ca. 14°51’07.26”N, 087°57’14.09”W], *A. Molina R. 10619* (EAP, F); camino entre Tapiquilares y Las Crucitas, 20 km S de San Antonio de Cortés, al pie de la montaña La Nieve, [ca. 14°59’22.86”N, 088°02’19.81”W], *C. Nelson et al. 8128* (MO). **Santa Bárbara**: eastern slopes of Cerro Santa Bárbara, [ca. 14°53’14.92”N, 088°07’01.01”W], *P. Allen et al. 6047* (CAS, EAP, F, GH, US); Cerro Sta. Bárbara, *R. Armour & A. Chable 6047* (BM, F); Punta Gorda, Lago Yojoa, 14°53’N, 088°00’W, *R. Evans 1001* (CAS); Punta Gorda, Lago Yojoa, 14°53’N, 088°00’W, *R. Liesner 26754* (MO).

6. *Louteridium koelzii* Miranda & McVaugh, *Ann. Inst. Biol. Mex.* 32:182. 1962 (“1961”). TYPE.— MEXICO. **Jalisco**: 8 mi SW of Pihuamo [ca. 19°11’26.09”N, 103°28’3.97”W], 500-600 m, 6-XII-1959 (flr), *R. McVaugh & W. Koelz 1507* (holotype: MICH!; isotype: MEXU!).

Trees to 10 m tall. Older (woody) stems subquadrate, irregularly fissured-striate; younger (herbaceous) stems stubby, quadrate, glabrous. Leaves deciduous, clustered at apex of old growth, petiolate, petioles to 73 mm long, blades membranaceous, ovate to elliptic, 90–220 mm long, 35–100 mm wide, 2–2.7 × longer than wide, acute to acuminate at apex, rounded to attenuate and asymmetric at base, surfaces glabrous, margin entire. Inflorescence of axillary and/or terminal subsessile to pedunculate thyrses (main axis with lateral pedunculate dichasia appearing as branches) to 250 mm long, peduncle to 50 mm long, pubescent with erect to flexuose eglandular trichomes 0.05–0.2 (–1) mm long, rachis pubescent with erect to flexuose eglandular trichomes 0.1–0.4 (–1) mm long; dichasia opposite, pedunculate, 1–3 (or more)-flowered, to 63 mm long (excluding corollas), dichasial peduncles 3–20 mm long, pubescent like rachis. Bracts caducous, lance-elliptic to elliptic, 12–17 mm long, 3.5–5 mm wide, abaxially pubescent with erect to flexuose eglandular trichomes 0.05–0.2 mm long. Bracteoles and secondary bracteoles usually present on young inflorescences but becoming deciduous as inflorescence matures, lance-elliptic to elliptic, 7–14 mm long, 2–3.5 mm wide, abaxially pubescent like bracts. Flowers pedicellate, pedicels 10–50 mm long, pubescent like rachis. Calyx 17–28 mm long, lobes subheteromorphic, membranaceous, abaxially pubescent with erect (to ± antrorse) eglandular trichomes 1–2 (–2.3) mm long, posterior lobe planar to ± conduplicate, ovate-elliptic, 17–25 mm long, 11–15 mm wide, usually slightly larger than lateral lobes, acuminate at apex, lateral lobes ovate-elliptic to elliptic to obovate, 15.5–22 mm long, 9–15 mm wide, rounded to acute at apex, veins of lobes prominent (ca. 9 major veins). Corolla “pale green” to greenish yellow, 50–55 mm long, externally glabrous, tube 29–33 mm long, narrow proximal portion 9–13 mm long, 9–16 mm in diameter near midpoint, throat 15–20 mm long, 30–35 mm in diameter at mouth, lobes spreading to recurved, “narrowly ovate to subcircular” (fide Miranda and McVaugh 1962), 18–24 mm long, 17–27 mm wide, rounded to acute at apex. Stamens 4, 72–90 mm long, filaments glabrous distally, pubescent proximally with eglandular trichomes, thecae 10–12 mm long; staminode (if present) not seen. Style 50–55 mm long, glabrous, stigma lobes 1.5 mm long, shape and width not determined. Capsule 25–30 mm long, 7–10 mm in diameter, pubescent throughout with erect to flexuose to antrorse eglandular trichomes 0.05–0.2 mm long, stipe 1.5–2 mm long. Seeds up to 16 per capsule, 7–8 mm long, 5–6 mm wide, surfaces minutely papillose.

Phenology.— Flowering: December–February; fruiting: February.

Distribution and habitat.— West-central Mexico (Jalisco, Michoacán; Fig. 8); plants occur on limestone slopes in “high forest dominated by *Brosimum*” in regions of tropical subdeciduous and deciduous forests at elevations from 500 to 1400 meters.

Illustrations.— Figure 14; Miranda and McVaugh (1962:183, fig. 2).

Conservation.— *Louteridium koelzii* is currently known from a very limited region of western Mexico (EOO = 5.3 km^2; AOO = 12 km^2). The species is not known to occur in a protected area, and it has not been recollected since 1975 (i.e., *McVaugh 26180*; although see discussion below about an undetermined plant from a nearby region of Jalisco). Based on current knowledge, there appear to be two subpopulations about 80 km apart, one in Jalisco and one in Michoacán. Comparing historic landsat images (2006 to 2017) via Google Earth Pro (2018) in the region of the known collections from Jalisco, it is evident that deforestation for agriculture has reduced the natural vegetation there substantially (ca. ≥ 30%), thus creating a threat to this species, at least in that region. No specific threat has been identified for the subpopulation in Michoacán. Thus, there are two locations for the species, and a threat is evident for one of them. Based on these observations, a preliminary conservation assessment of Endangered (EN; B1, a, b) is proposed for *L. koelzii*.

Discussion.— An undetermined specimen of *Louteridium* from western Mexico (Jalisco: Mpio. Jilotlán de los Dolores, Cerro de San Antonio, 15 km N de Tazumbos, matorral subtropical en suelos con pedregocidad de toba volcánica, 900 m, 6 Feb 1982, *F. Santana Michel 1081*, IBUG) does not seem to pertain to either species known from nearby regions (i.e., *L. brevicalyx* or *L. koelzii*) or other species of the genus. The plant, which lacks mature flowers, is geographically closest and morphologically most similar to *L. koelzii*. Like that species, it occurs in an apparently dry habitat and has seasonally deciduous foliage. Both of these characteristics suggest that the

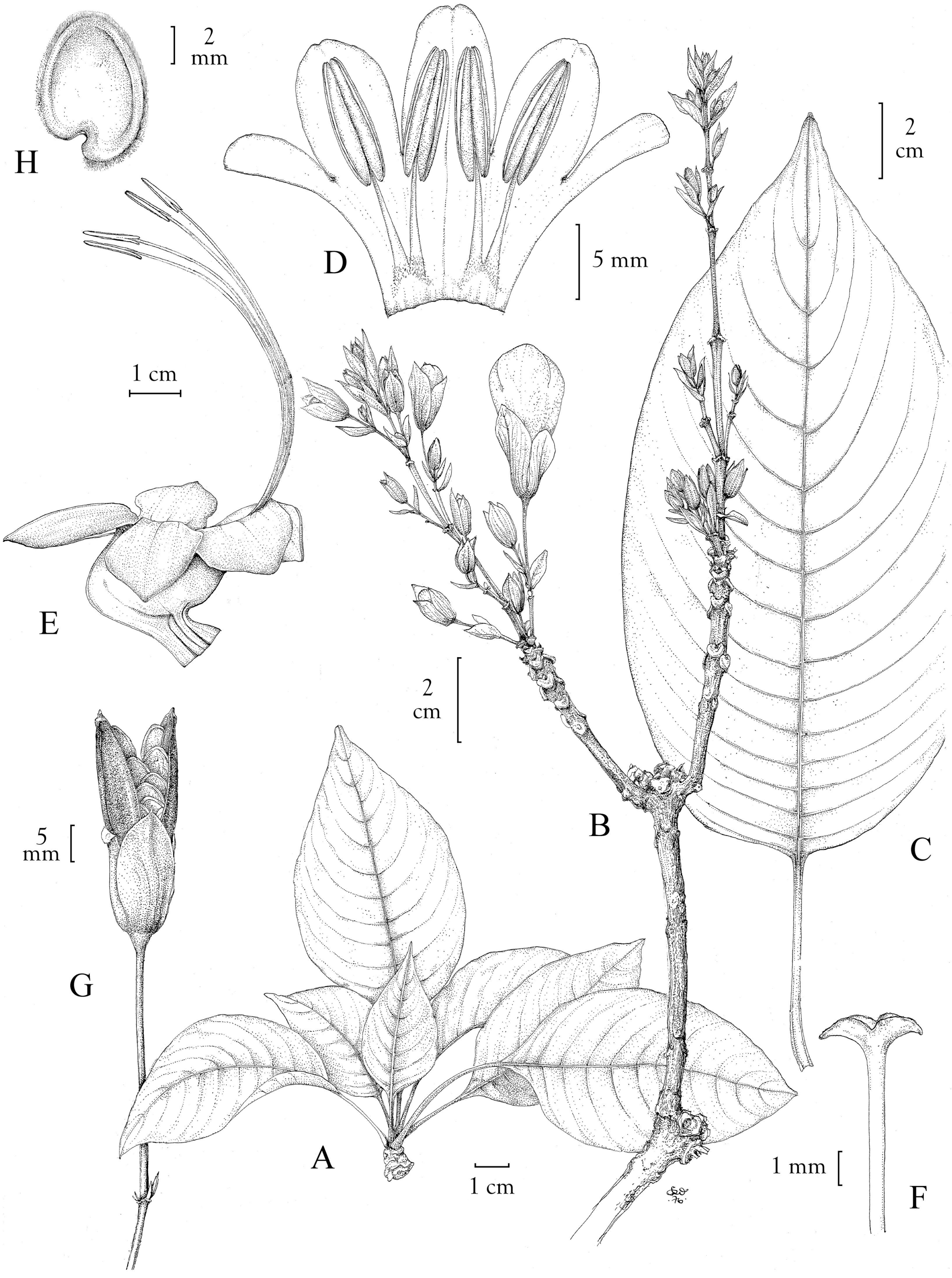

FIGURE 14. *Louteridium koelzii*. A. Apex of shoot with flush of new leaves (*McVaugh & Koelz 1797*). B. Branch with inflorescence in flower (*McVaugh & Koelz 1507*). C. Leaf (*McVaugh & Koelz 1797*). D. Corolla bud opened (*McVaugh & Koelz 1797*). E. Dehisced corolla with epipetalous stamens (*McVaugh 26180*). F. Distal portion of style and stigma (*McVaugh 26180*). G. Partially dehisced capsule with calyx and pedicel (*McVaugh 26180*). H. Seed (*McVaugh 26180*). Drawn by Karin Douthit, copyright reserved to University of Michigan Herbarium, used with permission.

undetermined plant has four stamens. Other characteristics in common with *L. koelzii* include erect to flexuose eglandular trichomes on the rachis, peduncles, and pedicels; ovate-elliptic calyx lobes, and externally glabrous corollas. It differs from specimens of *L. koelzii* studied herein by having pubescent young stems, shorter calyces (14–15 mm long, although the flowers are not fully mature), and longer (35–40 mm) capsules that are pubescent only at the apex. Disposition of this plant awaits further studies and/or collections.

ADDITIONAL SPECIMENS EXAMINED.— MEXICO. **Jalisco**: ca. 12–13 km SW of Pihuamo, *R. McVaugh 26180* (MICH); 8 mi SW of Pihuamo, *R. McVaugh & W. Koelz 1797* (MEXU, MICH, US). **Michoacán**: 15–16 km SE of Aserradero Dos Aguas, W of Aguililla [ca. 18°45'51.11"N, 102°49'22.26"W], *R. McVaugh 24740* (MICH).

7. *Louteridium mexicanum* (Baill.) Standl., *Contr. U.S. Natl. Herb.* 23:1338. 1926. *Neolindenia mexicana* Baill., *Bull. Mens. Soc. Linn. Paris* 2:851. 1890. TYPE.— MEXICO. **Veracruz or Chiapas**: "forêts humides de Zacualpan, Chiapas," II-1840 (flr), *J. Linden s.n.* (holotype: P!; isotypes: G!, K!). A collection number (*1637*) that is not on specimens at P and G, is on the specimen from Hooker's herbarium at K.

Louteridium conzattii Standl., *Contr. U.S. Natl. Herb.* 23:1338. 1926. TYPE.— MEXICO. **Oaxaca**: Distr. Tuxtepec, de Jalapa a La Raya, margen izquierda del Río Grande, [ca. 18°01'16.00"N, 096°34'25.98"W], 450 m, 3-XI-1919 (buds), *C. Conzatti 3788* (holotype: US-1014038!; isotypes: MEXU! US-1014039!).

Shrubs to trees to 12 m tall, terrestrial. Older (woody) stems subquadrate, irregularly striate-fissured, glabrous or glabrate; younger (herbaceous) stems quadrate to quadrate-sulcate, internodes glabrous or with sparse flexuose to antrorse eglandular trichomes to 0.5 mm long, nodes glabrous or with some flexuose eglandular trichomes to 0.5 mm long. Leaves not all seasonally deciduous, evenly distributed on new growth, petiolate, petioles to 220 mm long, blades membranaceous, broadly ovate to ovate to ovate-elliptic to elliptic to broadly elliptic, 40–360 mm long, 21–170 mm wide, 1.3–2.9 × longer than wide, acuminate to acute-apiculate to caudate at apex, acute to rounded to subcordate at base, adaxial surface glabrous, abaxial surface glabrous or pubescent along major veins with trichomes like those at nodes, margin ± entire to crenate. Inflorescence a terminal pedunculate (racemose thyrse to) thyrse to 390 mm long (including peduncle and excluding corollas), peduncle to 190 mm long, glabrous or pubescent like young stems, rachis glabrous or pubescent with flexuose to flexuose-antrorse eglandular trichomes 0.2–0.8 (–1) mm long (villous), trichomes sometimes restricted to nodes; dichasia modified by sympodial expansion into contracted to ± expanded unbranched or branched short-shoots to 25 (–46) mm long, opposite, subsessile to pedunculate, 3–many-flowered, to 120 mm long (excluding corollas), dichasial peduncles 1–22 mm long, glabrous or villous. Bracts often caducous, sessile to petiolate, ovate to lance-elliptic to linear, 20–48 mm long, 2–16 mm wide (or the proximalmost pair sometimes foliose and larger), abaxially glabrous or pubescent with antrorsely appressed eglandular trichomes. Bracteoles and secondary bracteoles usually persistent, lance-ovate to lanceolate to linear-lanceolate, 10–25 mm long, 1–8 mm wide, abaxially glabrous or pubescent with a few antrorsely appressed eglandular trichomes to 0.5 mm long along midvein or pubescent with latter type trichomes over entire surface. Flowers pedicellate, pedicels to 85 mm long, glabrous or villous. Calyx 17–39 mm long, lobes appearing distinct or fused at base for 1–2 mm, heteromorphic, ± membranaceous, abaxially appearing glabrous although covered with minute sessile glands (glandular punctate; punctations < 0.05 mm in diameter) and posterior lobe sometimes sparsely villous along keel, posterior lobe conduplicate, ovate, 16–36 mm long, ± equaling to slightly longer than lateral lobes, 9–14 mm wide, acute to attenuate to subfalcate at apex, lateral lobes lunate, 16–32 mm long, 6–12 mm wide, rounded to acute to subacuminate at apex. Corolla usually greenish and maroon (also described as white with purplish lobes and pale rose in plants from San Felipe Usila, Oaxaca; see discussion below), 38–54 mm long, externally puberulent with sessile to subsessile glands 0.05–0.1 mm long and often with glandular and eglandular trichomes to 0.2 mm long as well, tube (19–) 30–35 (–42) mm long, narrow proximal portion 8–14 mm long, 5–10 mm in diameter near midpoint, throat 15–23 mm long, 24–33 mm in diameter at mouth, lobes recoiled, subtriangular to broadly ovate to elliptic, 10–16 mm long, 8–14 mm wide, rounded at apex. Stamens 2, 60–77 mm long, filaments glabrous distally, pubescent proximally with eglandular trichomes, thecae 9–13 mm long; staminodes 2, 1–3 mm long. Style 72–85 mm long, glabrous (or sometimes with sessile to subsessile glands to 0.05 mm long near base), stigma subequally to unequally 2-lobed, lobes linear-elliptic to elliptic to obovate-elliptic, 1–3.8 mm long, 0.6–1.5 mm wide. Capsule 16–24 mm long, 4–8 mm in diameter, sparsely puberulent with sessile to subsessile glands to 0.05 mm long, stipe 1–2 mm long. Seeds up to 16 per capsule, 4–5.5 mm long, 3.5–5 mm wide, surfaces smooth or covered with subconic papillae.

PHENOLOGY.— Flowering: September–May; fruiting January–May. Based on greenhouse observations of *Breedlove & Daniel 70879gh*, corollas open after 17:00 and all fall by 11:00 the next morning.

DISTRIBUTION AND HABITAT.— Southern Mexico (Chiapas, Oaxaca, Puebla, Tabasco, Veracruz) and Guatemala (Alta Verapaz, Petén) (Fig. 11); plants occur on slopes and along watercourses on limestone (often karstic) in primary or secondary lowland rain forests (selva alta perennifolia), montane rain forests, cloud forests, and evergreen seasonal forests (including selva mediana subperennifolia) at elevations from 50 to 1200 m. The distribution of this species appears to be entirely on the versants of the Gulf of Mexico and the Caribbean Sea. Daniel et al. (2012) reported this species from Guatemala. Plants from Guatemala previously attributed to *L. mexicanum* pertain to *L. purpusii* (see discussion in Daniel 1995).

LOCAL NAMES.— “K’o’och batz’” (*Paniagua 539*); “oj-oj” (Kunkel 161); “palo aguañoso” (*Ramos & Martínez S. 620*); “sabal tzununte” (*Palacios E. 9631*); “Uc’o’och chuba’atsir wis” (*Levy T. & Durán F. 398*).

USES.— Leaves applied against the body for fever (*Wendt et al. 3614*); a drink made from the boiled leaves is used for “dolor orinar” (*Paniagua 539*).

ILLUSTRATIONS.— Figures 4E, 15.

CONSERVATION.— *Louteridium mexicanum* is the most commonly collected species in Mexico, and has an EOO of 35,531 km^2. At least nine protected areas are located entirely or partially within its EOO, and the species has been collected in two of them. Frequency data from herbarium collection labels varies from scarce to infrequent to common to abundant. Although unidentified threats are undoubtedly present in portions of its geographic distribution, a preliminary conservation assessment of Least Concern (LC) is proposed for this species.

DISCUSSION.— Daniel (1995) discussed the probable state from which the type was collected; this would appear to be Veracruz rather than Chiapas. Linden collected in both states (Ossenbach 2009), but no “Zacualpan” has been located in Chiapas (D. Breedlove, personal communication in 1994). Zacualpan (or Zacuapan or Zacuapam [ca. 19°12’46.44”N, 096°51’8.73”W], see Sousa S. 1969; not the town of Zacualpan at 20°26’1.71”N, 098°20’57.69”W in northwestern Veracruz), Carl Sartorius’ large hacienda located between Jalapa and Córdoba in west-central Veracruz, with its headquarters at El Mirador, is known to have been visited by several early Mexican collectors, including Linden (Ossenbach 2009). Because it is ca. 42 km north of the currently known distributional range of *L. mexicanum* (Fig. 11), and because of the ambiguity of the locality based on

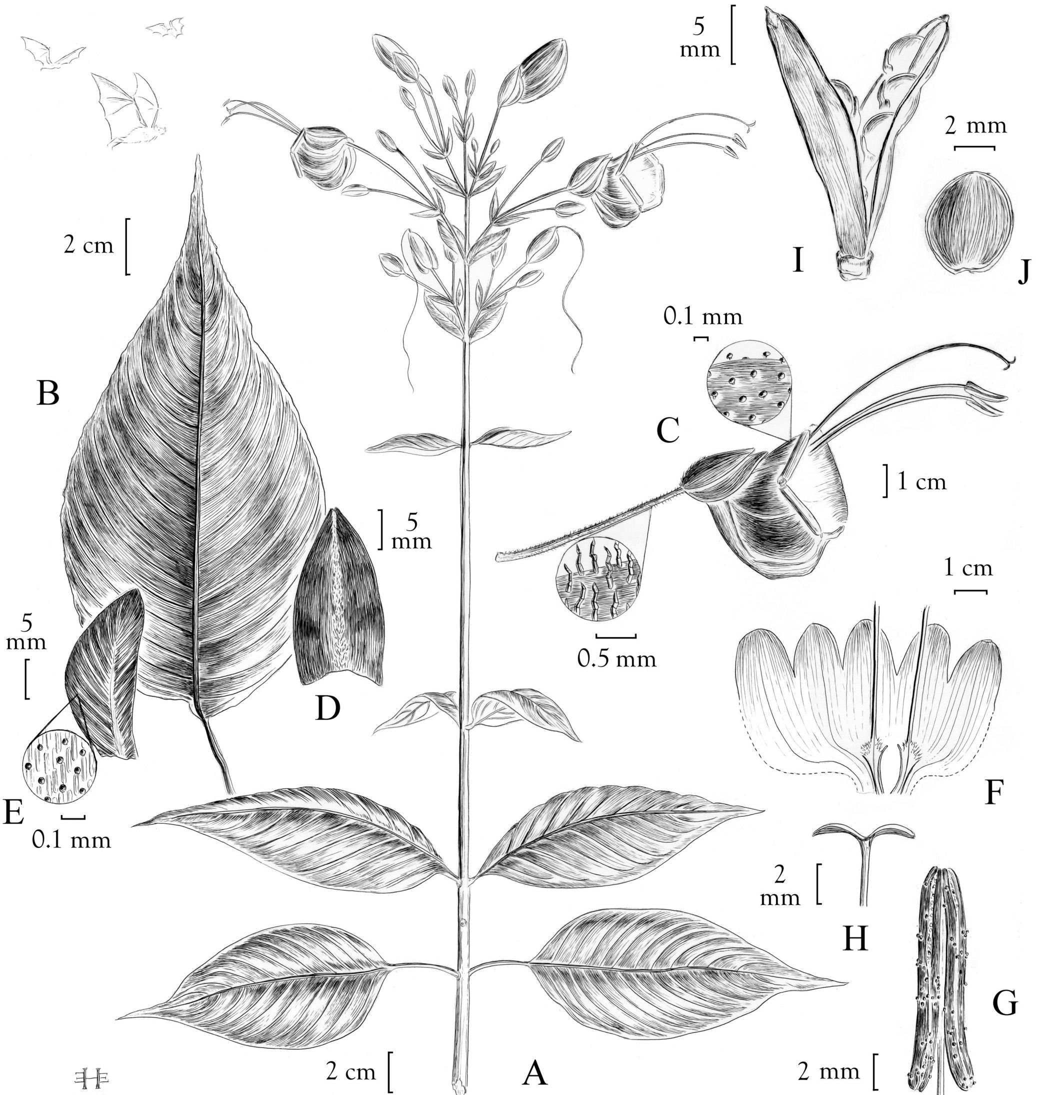

FIGURE 15. *Louteridium mexicanum*. A. Shoot with inflorescence in flower. B. Leaf. C. Flower with pedicel and enlargements showing glands on external surface of corolla and eglandular trichomes on pedicel. D. Posterior calyx lobe. E. Lateral calyx lobe (adaxial surface with enlargement showing glandular punctations and cystoliths). F. Corolla dissected to show insertion of stamens. G. Anther. H. Distal portion of style and stigma. I. Capsule. J. Seed. A-H from *Breedlove & Daniel 70879cv*, I from *Breedlove 24177*, J from *Hernández G. 1054*. Drawn by Erin Hunter (inverted from scratchboard).

Linden's indication of Chiapas on the collection labels, Zacuapam (shown in Fig. 11 with a question mark) is not included in the calculation of the EOO for the species.

Based on living flowers of *Breedlove & Daniel 70879cv*, the coloration of corollas of this species can be more fully described as follows: the narrow proximal portion of the tube (covered by the calyx) is green; the throat is green with maroon veins and tinged with maroon between the major veins; the lips (with recoiled lobes) are mostly maroon.

Daniel (1995) noted considerable variation in pubescence, leaf shape, bract persistence, and bract shape among specimens from Chiapas, Mexico. One of the two collections (*Breedlove 24803*, *Palacios E. 385*) that he indicated showed some intermediacy with *L. donnell-smithii* in pubescence was sampled in the phylogenetic analysis. *Palacios E. 385* was strongly supported as nested within the clade of other sampled plants of *L. mexicanum* (Fig. 1). Thus, both plants are here included within *L. mexicanum*.

Somewhat atypical plants from the vicinity of San Felipe Usila, Oaxaca (e.g., *Ibarra M. et al. 3758*, *3765*; *Calzada et al. 16579*) are distinctive by their long calyces (30–39 mm) with the posterior lobe conspicuously attenuate-falcate apically, corollas pale rose to white with purplish lobes and pubescent with glandular and eglandular trichomes to 0.2 mm long, and rachis (i.e., *Calzada et al. 16579*) often somewhat scurfy to minutely puberulent with sessile to subsessile glandular trichomes less than 0.05 mm long. In *Calzada et al. 16579*, the calyx and pedicels are like more typical specimens of *L. mexicanum*, and the rachis often has longer eglandular trichomes to 0.1 mm as well. Although similar calyces and trichomes on corollas are sometimes seen elsewhere among specimens of *L. mexicanum*, the corolla color of these collections appears to be unusual compared to other Mexican representatives of the species. However, corollas of *Foerther et al. 10940* from Guatemala are described as brownish violet. In pubescence of the rachis, these plants somewhat resemble *L. purpusii*. On the whole, they appear more like *L. mexicanum*, in which species they are treated here.

ADDITIONAL SPECIMENS EXAMINED.— MEXICO. **Chiapas**: Mpio. Ocosingo, 4.4 km SO de San Javier, 16°48'49"N, 091°04'04"W, *G. Aguilar M. et al. 4713* (MEXU); Mpio. Solosuchiapa, 2–4 km below Ixhuatán toward Pichucalco, [ca. 17°18'47.23"N, 093°00'11.57"W], *D. Breedlove 24177* (DS, ENCB, MO, NY), *29799* (DS, LL, MEXU, MICH, MO, RSA), *D. Breedlove & F. Almeda 56805* (CAS, ENCB, LL, NY); Mpio. Berriozábal, 13 km N of Berriozábal near Pozo Turripache and Finca El Suspiro, [ca. 16°52'25.01"N, 093°19'8.64"W], *D. Breedlove 24803* (DS, ENCB, MO), *D. Breedlove & T. Daniel 70879* (CAS), cultivated plants of this collection grown from cuttings in San Francisco, California, *70879cv* (CAS), *D. Breedlove & R. Thorne 30786* (DS, ENCB, MO), *D. Breedlove et al. 66158* (CAS); Mpio. Palenque, near Agua Azul, *D. Breedlove 56091* (CAS, LL, MEXU); Mpio. Ocosingo, near ruins of Bonampak at jct. road from Lacanjá to Echeverría and road from Chancalá, [ca. 16°48'04.57"N, 091°06'21.97"W], *D. Breedlove & F. Almeda 58020* (CAS, LL, MEXU, MO); Mpio. San Fernando, 20 km NW of San Fernando just beyond Colonia Cuahtémoc, [ca. 16°58'42.74"N, 093°20'28.46"W], *D. Breedlove & M. Bourell 68269* (CAS); Mpio. Ocosingo, 70 km SW of Palenque toward Ocosingo along the Jol Uk'um, [ca. 17°10'48.02"N, 092°06'39.86"W], *D. Breedlove & B. Keller 49526* (CAS, MEXU, MO); Mpio. Ocozocoautla de Espinosa, 26–28 km N of Ocozocoautla toward Mal Paso, [ca. 16°56'22.87"N, 093°27'55.46"W], *D. Breedlove & A. Smith 22469* (DS, MEXU, MICH, MO, RSA); Mpio. Ocosingo, 4 km E del crucero San Javier, 16°48'44"N, 091°03'13"W, *J. Calónico S. et al. 25022* (ENCB, MEXU); Mpio. Berriozábal, ca. 12 km NW of Berriozábal, ca. 16°51'N, 093°19'W, *T. Daniel 8375* (CAS, MEXU); Mpio. Ishuatán, carretera 195, 45 km N [S] de Pichucalco, [ca. 17°18'26.14"N, 093°00'27.05"W], *S. Gliessman 77-7* (MEXU); Mpio. Pichucalco, 20 km Teapa–Pichucalco, [ca. 17°32'45.83"N, 093°04'44.80"W], *M. Ishiki et al. 2035* (CAS); Mpio. Ocosingo, Lacandona de Lacanhá–Chansayab, 130 km SE de Palenque, por la carretera fronteriza hasta el crucero San Javier, después 8 km hacia el oeste, 16°44'N, 091°05'W, *S. Levy T. & A. Durán F. 398* (MEXU); Mpio. Berriozábal, 12 km N de Berriozábal, *E. Martínez S. & M. Soto 24216* (MEXU); Mpio. Ishuatán, 9 km N de Tapilula, [ca. 17°17'16.71"N, 093°00'38.70"W], *E. Martínez S. et al. 3198* (CAS, ENCB, MEXU, MO, WIS); Mpio. Yajalón, Yajalón–Petalsinco, carretera de terraceria KM 5, *A. Méndez T. [=A. Ton] 7134* (IEB, MEXU, MO, RSA, XAL); Mpio. Ocozocoautla, 9 km

NW de Emilio Rabasa, 500 m W de El Aguajito, 16°57’32”N, 093°40’31”W, *S. Ochoa G. 3860* (XAL); Mpio. San Fernando, cerros adelante de Col. Cuauhtémoc, [ca. 16°56’39.34”N, 093°13’33.83”W], *E. Palacios E. 385* (CAS); Mpio. Ocozocoautla, Reserva El Ocote, al O mas adelante de la caseta, *E. Palacios E. 9631* (CAS); Mpio. San Fernando, 1.4 km N de Cuauhtémoc, 16°56’32”N, 093°13’30”W, *R. Palestina 1747* (XAL); Mpio. Ocosingo, Lacanjá–Chansayab, Vereda de Pancho López Kin, *B. Paniagua 539* (MEXU); Mpio. Berriozábal, 13 km N de Berriozábal, *O. Téllez V. et al. 7591* (MEXU); Mpio. Yajalón, Yajalón–Petalzinco, [ca. 17°12’13.88”N, 092°23’17.85”W], *A. Ton 7134* (XAL); Mpio. Tila, Finca Morelia, [ca. 17°17’13.71”N, 092°26’08.79”W], *A. Ton 7427* (MEXU). **Oaxaca**: Mpio. San Pedro Ixcatlán, Cerro Camarón, al W de Cerro Quemado, *J. Calzada 10293* (XAL); Mpio. Chiltepec, Ejido de Rancho Faisán, vereda para La Rejoya, [ca. 17°56’57.43”N, 096°09’47.56”W], *J. Calzada 14456* (CAS, MEXU); Mpio. San Miguel Soyaltepec, Cerro Tepezcuintle, *J. Calzada & S. Anta 17515* (MEXU); Mpio. San Felipe Usila, 2 km del poblado Cerro Verde, carretera al campamento Arroyo Tambor, *J. Calzada et al. 16579* (MEXU); Distr. Tuxtepec, Presa Temazcal, camino Temazcal–Vertedor a 6 km, *L. Cortes & R. Torres C. 66* (ENCB, MEXU); Mpio. Soyaltepec, 2 km de la Hidroelectrica al Vertedor de la Presa Temascal, *L. Cortes & R. Torres C. 617* (MEXU); Distr. Tuxtepec, Mpio. Acatlán, Cerro Buenos Aires, lado oeste de la Presa Temazcal (Miguel Alemán), *L. Cortes et al. 165* (ARIZ, CAS, MEXU); Uxpanapa Region, E of Sarabia toward Uxpanapa, 4.2 mi NE of Río Corte, 17°09’N, 095°15’W, *T. Croat & D. Hannon 63176* (CAS, DUKE, MEXU, MO, TEX); Mpio. San Miguel Soyaltepec, Cerro Tepezcuintle, 18°09’34.1”N, 096°20’50.5”W, *C. Cruz E. & G. Juárez G. 2599* (MEXU, SERO); Mpio. Santa María Chimalapa, Matías Romero, Colonia Cuauhtémoc, [ca. 17°06’06.64”N], *A. Delgado S. 942* (ENCB, MEXU, US); Mpio. San Felipe Usila, Cerro Verde, [ca. 17°53’13.44”N, 096°30’05.71”W], *A. Hanan A. & R. de Santiago 854* (MEXU, SERO); Mpio. Santa María Chimalapa, ca. 10 km O de Sta. María por la vereda a Chicosaja, 16°53’N, 094°46’W, *H. Hernández G. 1054* (CAS, ENCB, MEXU, MO, XAL); Mpio. San Felipe Usila, Cerro Verde, 8 km NNE of San Felipe Usila, 17°57’N, 096°30’W, *G. Ibarra M. et al. 3758* (BM, MEXU, MO, SERO); Mpio. San Felipe Usila, Nueva Santa Flora, 17°55’N, 096°26’W, *G. Ibarra M. et al. 3765* (BM, MEXU, MO, SERO); Distr. Tuxtepec, Mpio. Ayotzintepec, 3.7 km NE de Ayotzintepec, Cerro Cueva de los Duendes, 17°42’26”N, 096°07’59”W, *G. Juárez G. 3771* (SERO); Mpio. Santa María Tlalixtac, Río Cóndor, brecha entre Santa María Tlalixtac y Chiquihuitlán de Benito Juárez, 17°57’14.5”N, 096°43’4.5”W, *G. Juárez G. & C. Cruz E. 937* (SERO, MEXU); Mpio. San Miguel Soyaltepec, Cerro Tepezcuintle, Papaloapam, 18°08’46.6”N, 096°21’37.3”W, *G. Juárez G. & A. Martínez F. 788* (SERO, MEXU); Mpio. Matías Romero, Río Coatzacoalcos at Cuauhtémoc, 18 km ESE of Palomares, 17°06’N, 094°53’W, *M. Nee 29710* (F, NY, XAL); Distr. Tuxtepec, “Cerro de la Cruz” near Temascal, E arm of Presa Alemán, 18°13’N, 096°24’W, *D. Neill 5399* (CAS, MEXU, MO); Mpio. Santa María Jacatepec, predio La Joya del Obispo, [ca. 17°51’33.80”N, 096°11’53.88”W], *C. Ramos & E. Martínez S. 620* (MEXU); Santa María Chilchotla, Cuahtémoc, ca. 4 km NE of Santa María Chilchotla, near Clemencia and Sta. Rosa, 18°14’N, 096°50’W, *S. Solheim & S. Reisfield 1363* (MEXU, NY, XAL, WIS); Mpio. San Pedro Ixcatlán, Sierra Mazateca, Cerro Camarón, 1 km E of village of Cerro Quemado, 18°09’N, 096°35’W, *S. Solheim & S. Reisfield 1499* (MEXU, XAL, WIS); Distr. Tuxtepec, Presa Miguel Alemán, Cerro de la Cruz, [ca. 18°12’20.03”N, 096°25’35.09”W], *R. Torres C. et al. 2133* (MO); Distr. Tuxtepec, Mpio. Santa María Jacatepec, camino a Cosolapa San Antonio, Ejido de San Felipe Tilpa, 13.3 km SO de La Reforma, 17°51’N, 096°03’W, *R. Torres C. & L. Cortes A. 11480* (CAS, MEXU); Mpio. Santa María Jacatepec, bajada del predio El Aguila a San Agustín, entrada por La Reforma, 28 km SW de Tuxtepec, carr. a Matías Romero, 17°50’N, 96°06’W, *R. Torres C. & E. Martínez S. 11093* (IEB, MEXU, MO, TEX); Mpio. Matías Romero, 7.2 km O de Esmeralda, 17°08’N, 094°50’W, *T. Wendt et al. 3614* (ARIZ, CAS, ENCB, LSU, MEXU, MO, NY, TEX, XAL). **Puebla**: Mpio. San Sebastián Tlacotepec, 18°26’12”N, 096°50’31.8”W, *L. Caamaño O. 6602* (HUAP-image seen). **Tabasco**: Mpio. Teapa, 0.34 km E de la Univ. Aut. Chapingo, 17°31’31”N, 092°55’33”W, *J. Calónico S. et al. 21459* (BM, MEXU); Mpio. Teapa, Cerro del Madrigal, 3 km E de Teapa, camino a Talcotalpa, 17°35’42”N, 092°55’26”W, *R. Fernández N. 2214* (ENCB, RSA); Mpio. Teapa, Sierra El Madrigal, Centro Regional Tropical Puyacatengo de la Univ. Autónoma de Chapingo, 17°31’02”–17°32’30”N, 092°54’10”–092°56’W, *A. Hanan A. et al. 326* (MEXU); Mpio. Tacotalpa, 3.2 km después de cruzar la panga del Río Oxiolotán, yendo de Tapijulapa a Oxoiotán, 17°26’30”N, 092°45’30”W, *S. Hernández & A. Espejo 139* (ENCB, IEB, MEXU, MO, XAL); Mpio. Macuspana, Parque Nac. Agua Blanca, KM 64 carretera Villahermosa–Escárcega, 17°38’N, 092°30’W, *M. López P. et al. 3* (ENCB, XAL); Mpio. Teapa, KM 6 de la entrada al ejido La Unión hacia Ixtapangajoya, [ca. 17°33’34”N, 092°57’39”W], *M. Magaña & A. Suárez F. 724* (ENCB, MEXU, XAL); Mpio. Macuspana, Centro Recreativo Agua Blanca, [ca. 17°41’15”N, 092°27’42”W], *M. Magaña et al. 1198* (ENCB, MEXU, XAL); Mpio. Macuspana, Parque Nac. Agua Blanca, KM 64 carretera Villahermosa–Escárcega, 17°38’N, 092°30’W, *L. Martínez G. 12* (ENCB, MEXU); Mpio. Teapa, Cerro Madrigal, 500 m E de Puyacatengo, Univ. Aut. Chapingo, 17°31’34”N, 092°55’17”W, *E. Martinez S. et al. 34736* (BM, MEXU); Mpio. Teapa, 1 km NE de Puyacatengo, 17°31’39”N, 092°55’22”W, *E. Martínez S. et al. 34899* (BM, BR, CAS, FLAS, MEXU, PH); Mpio. Teapa, El Azufre, 16 km E de Teapa, 17°35’N, 092°50’W, *P. Tenorio L. et al. 5577* (ARIZ, MEXU, RSA, TEX); Mpio. Macuspana, Agua Blanca, *F. Ventura A. 20941* (CAS, ENCB, IEB, MEXU, NY); Mpio. Teapa, El Madrigal, 17°35’07”N, 092°56’21”W, *F. Ventura A. 20989* (ENCB, MEXU, NY, XAL); Mpio. Macuspana, Agua Blanca, *S. Zamudio 183* (XAL). **Veracruz**: Mpio. Cuichapa, carretera de terracería entre Cuichapa y Omealca [ca. 18°45’51.96”N, 096°49’53.57”W], *J. Calzada & A. Vovides 2396* (ENCB, F, MEXU, MO, XAL); Mpio. Jesús Carranza, KM 6 del camino Cedillo–Río Alegre, 17°10’N, 094°40’W, *B. Dorantes 3917* (ENCB, MEXU, XAL); Mpio. Hidalgotitlán, kms 0–2 del camino Plan de Arroyos–Alvaro Obregón, 17°15’N, 094°40’W, *J. Dorantes et al. 2801* (ENCB, F, NY, XAL); Mpio. Hidalgotitlán, 0–2 km del Campo Cedillo, rumbo a Río Alegre, 17°19’N, 094°40’W, *J. Dorantes et al. 2936* (F, XAL); Mpio. Jesús Carranza, KM 10 del camino Cedillo–Fco. Villa, 17°10’N, 094°40’W, *J. Dorantes et al. 3938* (ENCB, F, MEXU, MO, XAL); Mpio. Hidalgotitlán, camino Cedillo–La Laguna, *J. Dorantes et al. 4138* (F, MEXU, XAL); Mpio. Tezonapa, 5–6 km SE de Motzorongo, 18°40’N, 096°40’W, *R. Gobles G. 208* (XAL), *299* (XAL); Mpio. Hidalgotitlán, 3 km SW of Campamento La Laguna, 17°16’N, 094°32’W, *M. Nee 29995* (F, MEXU, NY, XAL); Mpio. Amatlán de los Reyes, Cerro de Amatlán [ca. 18°49’53.93”N, 096°54’3.08”W], *H. Oliva & V. Villar 624* (IBUG, XAL); Mpio. Coetzala, 1 km E de Coetzala, 18°46’50”N, 096°54’52”W, *A. Rincón G. & C. Durán E. 1508* (MEXU, XAL); Mpio. Hidalgotitlán, Río Soloxuchil, entre Hnos. Cedillo y La Escuadra, 17°17’N, 094°38’W, *M. Vásquez et al. 322* (F); Mpio. Hidalgotitlán, brecha Hnos. Cedillo–La Laguna, *B. Vázquez 17* (F, MEXU, NY, XAL); Mpio. Jesús Carranza, 3 km E del Río Chalchijapa por la carretera Sarabia–Cedillo, *M. Vázquez T. 1585* (XAL); Mpio. Jesús Carranza, 2 km N del Poblado 2, Ejido F.J. Mina, 17°16’N, 094°40’W, *M. Vázquez T. et al. V-2568* (CAS, MEXU, XAL); Chicomapa [ca. 18°33’39, 096°51’08”W], *V. Vázquez T. 548* (ENCB, F, IEB, MEXU, XAL). GUATEMALA. **Alta Verapaz**: Mpio. Rubeltein, Montaña Sacranix, Wegstrecke zwischen der Finca Xalcata (= Saqmoc) und der Finca Sacté, S des Río Sachichaj (W der Strasse Cobán–Chisec), *H. Foerther et al. 10940* (BM, W); Sacté, 15°30’N, 090°27’W, *I. Kunkel 161* (BR).

8. *Louteridium parayi* Miranda, *Ceiba* 4:140. 1954. **Type**.— MEXICO. **Chiapas**: cerca del Suspiro, unos 9 km NO de Berriozábal [ca. 16°52'36.21"N, 093°19'34.53"W], 950 m, selva alta siempre verde, 9-VI-1953 (flr, frt), *L. Paray & F. Miranda 7834* (holotype: MEXU-00029822!; isotypes: F!, MEXU-00029828!).

Shrubs or trees to 3 m tall, epiphytic or epipetric. Older (woody) stems subquadrate to subterete, lenticellate, lacking trichomes; younger (herbaceous) stems quadrate-sulcate, glabrous. Leaves not all seasonally deciduous, evenly distributed along stems, petiolate, petioles to 20 mm long, blades coriaceous-subsucculent, oblanceolate to obovate, 50–200 mm long, 15–63 mm wide, 3.3–5 × longer than wide, acute-apiculate (to caudate) at apex, attenuate to long-attenuate at base, adaxial surface glabrous, abaxial surface with scattered flexuose to antrorse eglandular trichomes to 1 mm long (or sometimes nearly glabrous), margin entire. Inflorescence a terminal pedunculate thyrse to 27 cm long (including peduncle and excluding corollas), peduncle 3.5–15 cm long, glabrous, rachis glabrous; dichasia modified by sympodial expansion and appearing like dichotomous branches with zig-zag nodes, alternate, pedunculate, 1–many-flowered, to 100 mm long (excluding corollas), dichasial peduncles to 55 mm long, glabrous. Bracts caducous, lance-ovate to elliptic, 7–15 mm long, 4–8 mm wide, abaxially glabrous. Bracteoles and secondary bracteoles persistent, ovate to ovate-elliptic to broadly elliptic, 6–11 mm long, 5–7.5 mm wide, abaxially glabrous (or inconspicuously glandular-punctate), those of a pair connate along one side for up to 1/2 their length and proximally subsaccate, sometimes conspicuously imbricate. Flowers pedicellate, pedicels to 30 mm long, glabrous. Calyx 24–39 (–48 in fruit) mm long, lobes heteromorphic, apparently subsucculent, abaxially glabrous, posterior lobe conduplicate, oblong to subelliptic to oblanceolate, 22–45 mm long, longer than lateral lobes, 7.5–14 mm wide, saccate or with a flap-like appendage to 2.5 mm long at base, rounded to acute at apex, lateral lobes lance-ovate to lance-linear to linear-oblong, 19–44 mm long, 5–8.8 mm wide, acute at apex. Corolla pale greenish, 45–72 mm long, externally glabrous, tube 25–35 mm long, narrow proximal portion of tube 0.5–3 mm long, 6–8.5 mm in diameter near midpoint, throat 24–33 mm long, 28–40 mm in diameter at mouth, lobes spreading to recurved, subtriangular to broadly ovate, 8–21 mm long, 10–17 mm wide, rounded and emarginate at apex. Stamens 2, 70–90 mm long, filaments glabrous distally, densely pubescent at base with eglandular trichomes, thecae 13–17 mm long; staminodes (if present) not seen. Style 74–90 mm long, glabrous, stigma unequally 2-lobed, lobes ovate to linear-elliptic to linear-oblanceolate, 2.5–6 mm long, 1.1–2.8 mm wide. Capsule 27–40 mm long, 5.5–7.2 mm in diameter, glabrous, stipe 5–13 mm long. Seeds up to 18 per capsule, 4.5–5 mm long, 4.3–4.5 mm wide, surfaces smooth or with irregular ridges.

Phenology.— Flowering: April–December; fruiting: June–December. Flowers of *Daniel & Wendt 5804* were observed to be fully open after dark.

Distribution and habitat.— Southern Mexico (Chiapas, Veracruz; Fig. 8); plants occur on slopes on limestone (often karstic) in lowland rain forests, lower montane rain forests, and montane rain forests at elevations from 100 to 1500 meters.

Illustrations.— Figures 4G, H, 16; Miranda (1954:141).

Conservation.— *Louteridium parayi* has an EOO of 2,210 km^2. Plants occur in at least one large protected area in Chiapas, and the EOO includes another small one in Verazcruz. Frequency information on collections varies from locally infrequent to locally frequent. Known occurrences reveal two subpopulations separated by ca. 110 km. Historical landsat imagery (1984 to 2017) via Google Earth Pro (2018) reveals that the habitat of the western subpopulation in the Uxpanapa region of Veracruz has undergone extensive conversion from forested land to local agriculture and pasturage. The same imagery does not clearly show a similar large-scale conversion of forest in the

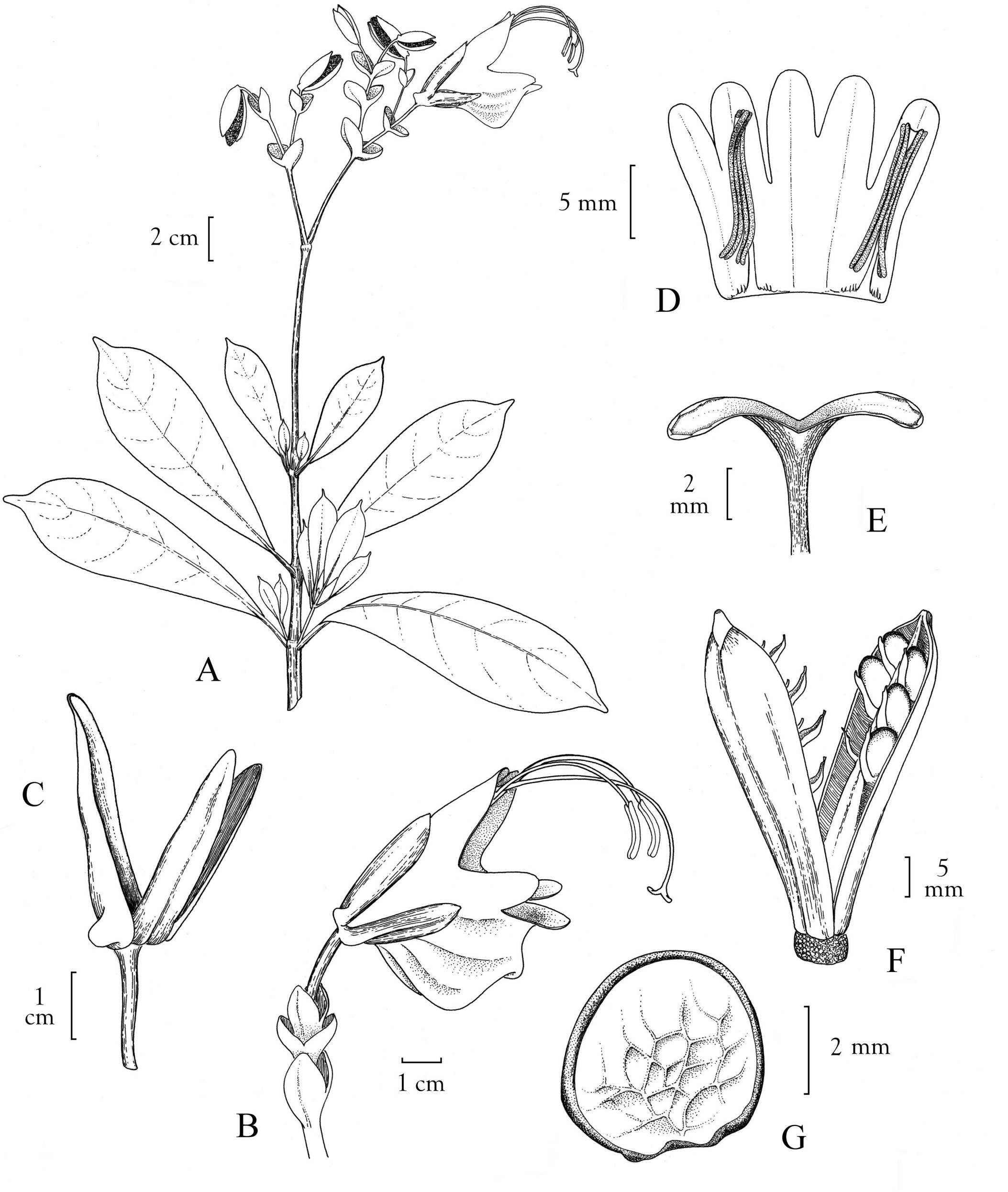

FIGURE 16. *Louteridium parayi*. A. Habit (*Breedlove 67024*). B. Bracteoles and flower (*Breedlove & Thorne 30789*). C. Calyx (*Breedlove 28970*). D. Corolla bud opened to show stamens (*Breedlove 67024*). E. Stigma (*Breedlove 67024*). F. Dehisced capsule (*Breedlove 28970*). G. Seed (*Breedlove 28970*). Drawn by Ellen del Valle.

region of the eastern subpopulation in Chiapas. Thus, there are two locations, in one of which a threat is evident. Based on these data, a preliminary conservation assessment of Endangered (EN; B1, a, b; IUCN 2017) is proposed.

DISCUSSION.— Although a single specimen was cited in the protologue, and Miranda (1954:125) indicated that the types of plants described in his publication were deposited at MEXU, there are two specimens of *Paray & Miranda 7834* in that herbarium. On one of them, "tipo" is written in the same handwriting as the rest of the label (i.e., by Miranda), and in his 1955 note on this specimen Miranda indicated that flowers and part of the inflorescence were lost from the specimen. In his note, he also refers to the isotype, which contains flowers and an inflorescence. Therefore, it seems clear that the sheet bearing "tipo" is the holotype, as indicated above.

Louteridium parayi is perhaps the most morphologically distinctive species in the genus. It possesses several unusual or unique characteristics: posterior lobe of the calyx subsaccate or with a basal appendage to 2.5 mm, a highly modified inflorescence, fused and basally subsaccate bracteoles, narrow proximal portion of the corolla tube very short to nearly nonexistent, and leathery oblanceolate to obovate leaves. The modified inflorescence of this species appears to be a thyrse, but because the lateral and modified dichasia are alternate (i.e., only one per node of the rachis), the thyrse appears dichotomously branched. The major branches in the inflorescence are interpreted as dichasial lateral branches that expand through non-symmetrical sympodial growth into often elongate and somewhat zig-zag "dichasial shoots." The inflorescence terminates in a dichasium.

Although no staminodes were seen in several dissections of corollas, it is possible that one or more small appendagelike staminodes could not be discerned among the dense trichomes at the base of the filaments. Indeed, an aberrant bud with extra corolla lobes possessed three fully formed stamens.

Additional specimens examined.— MEXICO. **Chiapas**: Mpio. Berriozábal, 13 km N of Berriozábal near Pozo Turipache and Finca Suspiro, [ca. 16°52'10.30"N, 093°17'21.61"W], *D. Breedlove 20260* (DS), *24816* (DS, F, MICH, MO, NY, RSA), *26336* (DS, ENCB), *67024* (BR, CAS, MEXU, MO, US), *D. Breedlove & T. Daniel 70889* (CAS), *D. Breedlove & R. Thorne 30789* (DS, ENCB, LL, MO); Mpio. Ocozocoautla de Espinosa, 30 km NW of Ocozocoautla, Cerro del Ocote, [ca. 16°55'51.78"N, 093°28'15.37"W], *D. Breedlove 28970* (DS, ENCB); Mpio. Ocozocoautla, Reserva del Ocote, Cerro La Colmena, al NE del Rancho Corocito, *J. Calzada et al. 9623* (F, MEXU, XAL); Mpio. Berriozábal, entre Col. Vista Hermosa y Rancho Flor de Corazón, [ca. 16°54'25.98"N, 093°26'56.10"W], *E. Palacios E. 1727* (CAS, IBUG, MEXU); El Suspiro, cerca de Berriozábal, [ca. 16°50'33.95"N, 093°18'07.62"W], *L. Paray 204* (ENCB); Mpio. Ocozocoautla de Espinosa, Cerro El Banadero, 7 km carr. Horizonte–El Ciprés, 16°53'N, 093°32'W, *F. Vázquez B. 952* (MEXU, XAL). **Veracruz**. Mpio. Jésus Carranza, Zona de Uxpanapa, ca. 1 km S of Sarabia–Uxpanapa road toward pueblo of Río Alegre, [ca. 17°12'07.46"N, 094°41'34.34"W], *T. Daniel & T. Wendt 5804* (CAS, DUKE, K, MEXU, MICH); Mpio. Minatitlán, Zona de Uxpanapa, 13.7 km E of La Laguna toward Uxpanapa, then 6.5 km N toward Belisario Domínguez, [ca. 17°18'47.80"N, 094°23'55.68"W], *T. Daniel & T. Wendt 5805* (CAS); Mpio. Hidalgotitlán, Hnos. Cedillo–La Escuadra, por el Río Soloxuchil, 17°16'N, 094°37'W, *B. Dorantes 957* (ENCB); Mpio. Hidalgotitlán, 0–2 km del camino Plan de Arroyios–Alvaro Obregón, 17°15'N, 094°40'W, *B. Dorantes 2850* (F, XAL); Mpio. Hidalgotitlán, KM 3 camino a La Escuadra, 17°15'N, 094°40'W, *B. Dorantes 3466* (ENCB, XAL); Mpio. Hidalgotitlán, KM 2 Plan de Arroyo–Río Alegre, 17°15'N, 094°40'W, *J. Dorantes 3040* (ENCB, IBUG, IEB, MEXU, XAL); Mpio. Hidalgotitlán, Camino Campto. Hnos. Cedillo–Plan de Arroyo, *J. Dorantes 3625* (XAL, WIS); Uspanapas, 14 km E of Campamento La Laguna (Poblado D.S.), 7.5 km N along small road through rubber plantation, [ca. 17°18'48.43"N, 094°23'56.21"W], *B. Hammel & M. Merello 15573* (CAS, ENCB, MO); Mpio. Uxpanapa, a 13.8 km E de La Laguna por la terracería a Uxpanapa, luego 6.8 km N por el camino a Belisario Domínguez, 17°18'48"N, 094°23'56"W, *M. Ishiki et al. 2230* (K, MEXU, US); Mpio. Hidalgotitlán, Hnos. Cedillo–La Escuadra por el Río Soloxuchil, 17°16'N, 094°37'W, *M. Vázquez T. 957* (ENCB, UC, XAL); Mpio. Jésus Carranza, 2 km N del Poblado 2, Ejido F.J. Mina, 17°16'N, 094°40'W, *M. Vázquez 2617* (CAS), *M. Vázquez et al. V-2566* (CAS, MEXU, MO, XAL); Mpio. Minatitlán, 6.6 km N de la terracería La Langua–Río Grande, sobre el camino nuevo a Ejido Belisario Domínguez, el cual sale de la terracería 14.7 km E de La Laguna, 17°20’N, 094°22’W, *T. Wendt & A. Villalobos C. 2540* (CAS, ENCB, LSU, MEXU).

9. ***Louteridium purpusii*** Brandegee, *Univ. Calif. Publ. Bot.* 6:68. 1914. **Type.**—MEXICO. **Chiapas**: Finca Irlanda [ca. 15°10’24.94”N, 092°20’10.22”W], VIII-1913 (flr, frt), *C. Purpus 6969* (holotype: UC!; isotypes: BM!, EAP-image seen, F!, GH!, MO!, NY!, US!, Z-image seen).

Shrubs or trees to 9 m tall, terrestrial. Older (woody) stems subquadrate-sulcate, ± scurfy and lenticellate, often puberulent like young stems; younger (herbaceous) stems quadrate to quadrate-sulcate and ± irregularly striate, glabrous or ± evenly puberulent with erect to retrorse to antrorse eglandular trichomes to 0.05 mm long. Leaves apparently not all seasonally deciduous, ± evenly distributed along young stems, petiolate, petioles to 40 mm long, blades membranaceous, ovate-elliptic to obovate-elliptic to obovate, 130–380 mm long, 40–115 mm wide, 2.1–4.3 × longer than wide, acuminate to acute-apiculate at apex, acute to attenuate at base, adaxial surface glabrous or puberulent like young stems, abaxial surface paler than abaxial surface, glabrous or pubescent with mostly antrorse eglandular trichomes 0.05–0.1 mm long along major veins, margin often undulate, entire to sinuate to crenate to crenate-dentate. Inflorescence a terminal pedunculate raceme to racemose thyrse to 63 cm long (including peduncles and excluding corollas), peduncle to 20 cm long, glabrous or pubescent like young stems, rachis puberulent with (retrorse to) erect to flexuose to antrorse eglandular trichomes to 0.05 mm long; dichasia modified by very short expansion between pairs of succeeding flowers with the congested dichasial axis becoming a ± fan-shaped to multi- and tortuously-branched racemelike lateral short-shoot to 15 mm long, opposite (and alternate?), sessile to subsessile, 3–many-flowered, to 60 mm long (excluding corollas), dichasial peduncles (if present) to 2 mm long, pubescent like rachis. Bracts caducous, not seen. Bracteoles and secondary bracteoles caducous, lance-linear to linear-elliptic, 5–13 mm long, 1–2.5 mm wide, abaxially pubescent like rachis. Flowers pedicellate, pedicels to 55 mm long, puberulent with erect to retrorse (to antrorse) eglandular trichomes to 0.05 mm long. Calyx 22–40 mm long, lobes distinct or fused at base up to 1 mm, heteromorphic, membranaceous, abaxially puberulent like pedicels and sometimes with a few sparse stipitate glands up to 0.2 mm long as well, also inconspicuously glandular-punctate, posterior lobe conduplicate, ovate to elliptic to obovate, 21–38 mm long, slightly shorter than to slightly longer than lateral lobes, 8.5–15 mm wide, acuminate to falcate at apex, lateral lobes sublunate, 22–37 mm long, 6–9 mm wide, acute to subfalcate at apex. Corolla cream to yellow-greenish and tinged with maroon, 45–52 mm long, externally pubescent with stipitate glandular trichomes 0.05–0.3 mm long (sometimes with flexuose eglandular trichomes to 0.2 mm long on or near margins of lobes as well), tube 25–33 mm long, narrow proximal portion 3–5 mm long, 7 mm in diameter near midpoint, throat 22–30 mm long, 25–35 mm diameter at mouth, lobes spreading to recurved, triangular to ovate, 12–21 mm long, 10–13 mm wide, rounded at apex. Stamens 2, 65–75 mm long, filaments glabrous distally, pubescent proximally with eglandular trichomes, thecae 10–12 mm long; staminodes (if present) not seen. Style 85–92 mm long, glabrous distally (not seen proximally), stigma equally 2-lobed, lobes elliptic, 1.4–2 mm long, width not determined. Capsule 22–30 mm long, 5–7.5 mm in diameter, densely pubescent with stipitate glandular trichomes (0.05–) 0.1–0.4 mm long, stipe 3–3.5 mm long. Seeds up to 12 per capsule, 4.5–5.2 mm long, 4.5–5 mm wide, surfaces smooth.

Phenology.— Flowering and fruiting: August–March.

Distribution and habitat.— Southern Mexico (Chiapas), Guatemala (Fig. 10); plants occur in wooded ravines in montane rain forests on the Pacific versant at elevations from 600 to 2000 m.

Illustration.— Figure 4F.

Local name.— “palo de agua,” (*Quarles van Ufford 137*).

Conservation.— *Louteridium purpusii* has an EOO of 944 km^2. Two prominent threats are evident throughout most or all of its known distribution, coffee agriculture and volcanic eruptions. Numerous active volcanos lie within and adjacent to the entire EOO of this species. Most of the occurrences of the species are within the prime growing elevations (i.e., 900 to 1800 m) for *Coffea arabica* L., and within two important coffee-growing regions (the Soconusco region of Chiapas, Mexico and the departments of San Marcos and Quetzaltenango in Guatemala). Mexico and Guatemala are two of the top 10 coffee-producing countries in the world (Anonymous 2003, 2018). Increasing demand for coffee worldwide (e.g., Lorenzetti 2016) has or could result in increased conversion of natural vegetation in the EOO of this species to agriculture. Thus, coffee production would appear to be the more immediate threat to *L. purpusii*. However, based on either threat, there would appear to be a single location for the species. A preliminary conservation assessment of Endangered (EN; B1, a, b; IUCN 2017) is proposed for this species.

Discussion.— This species resembles some plants of *L. mexicanum* (see discussion under that species), but differs by its more obovate leaves and pubescence. Additional morphological tendencies that distinguish these species include the more racemose (vs. thyrsoid) inflorescences of *L. purpusii* (with dichasial peduncle lengths of 0 to 2 (vs. 1 to 22) mm; the caducous bracteoles (vs. usually persistent in *L. mexicanum*); and the generally longer styles (85 to 92 vs. 72 to 85 mm long), capsules (22 to 30 vs. 16 to 24 mm long), and capsular stipes (3 to 3.5 vs. 1 to 2 mm long). The distributional ranges of these two species are not known to overlap and are restricted to different versants of Mexico and Guatemala.

Additional specimens examined.— MEXICO. **Chiapas**: Mpio. Unión Juárez, 17 km E of Cacahoatán [ca. 15°1’56.19”N, 092°5’27.65”W], *D. Breedlove & A. Smith 31613* (DS, MEXU, MO); Finca Nubes [ca. 15°03’43.30”N, 092°08’39.20”W], *F. Miranda 1723* (LL, US); from [Finca San Antonio] Chicharras, *E. Nelson 3749* (US); Finca San Antonio [Chicharras; ca. 15°7’26.12”N, 092°14’45.30”W], *L. Quarles van Ufford 137* (U). GUATEMALA. **Quezaltenango**: Sta. María Ikibál [not located, possibly Santa María de Jesús], *C. Bernoulli & O. Cario 2254* (K); lower S slope of Volcán Santa María, 0.3 mi W of jct. Finca Pirineos road with hwy. 95 at KM 97 [ca. 14°41’5.41”N, 091°32’50.04”W], *C. Broome 728* (CAS, DUKE, F, MICH, US); de la represa de Santa María al Volcán Pecul [ca. 14°43’26.73”N, 091°30’42.09”W], *Equipo CECON 1063* (MO); San José Buena Vista, Costa Cuca, [ca. 14°41’53.74”N, 091°46’35.82”W], *L. Rodríguez 444* (P); Palmar, [ca. 14°39’12.22”N, 091°35’25.38”W], *A. Skutch 1451* (F, US); Finca Pireneos, below María de Jesús, [ca. 14°41’38.02”N, 091°32’30.77”W], *P. Standley 68259* (F, US); along old road between Finca Pirineos and Patzulín, *P. Standley 86714* (F); *86726* (F), *86749* (F), *86750* (F, US), *86763* (F); along Quebrada San Gerónimo, Finca Pirineos, lower S-facing slopes of Volcán Santa María, between Santa María de Jesús and Calahuaché, *J. Steyermark 33435* (F); off Hwy. 95 at KM 197, old road to Finca Pirineos, ca. 0.5 mi from main hwy., *D. Stone 3086* (DUKE); Colomba, Finca San Francisco Pie de la Cuesta, 14°43’41.05”N, 091°43’04.45”W, *L. Velásquez & W. López 1792* (CAS). **San Marcos**: Finca El Porvenir along Río Chopal, S-facing slopes of Volcán Tajumulco [ca. 14°57’36.58”N, 091°56’40.73”W], J. *Steyermark 37501* (F); El Tumbador, finca Nueva Granada, 14°51’19.9”N, 091°53’05.9”W, *L. Velásquez et al. 658* (BIGU, CAS).

10. *Louteridium rzedowskianum* T.F. Daniel, *Proc. Calif. Acad. Sci.* 64:144. 2017. *Louteridium brevicalyx* Rzed., *Ciencia (México)* 28:53. 1973, nom. inval., non *Louteridium brevicalyx* A. Richardson (1972). *Louteridium rzedowskii* T.F. Daniel, *Madroño* 31:91. 1984, nom. inval. **Type**.— MEXICO. **Guerrero**: Mpio. Chilpancingo, Rincón de la Vía, cerca de Agua de Obispo [ca. 17°17’45.05”N, 099°28’17.54”W], 750 m, 19-I-1964 (flr), *H. Kruse 1380* (holotype: ENCB-002790-shoots bearing flowers only-image seen; isotypes (shoots bearing flowers only): EAP!, ENCB-002789!, FCME!, MEXU!, MICH!, MO!, US!).

Shrubs to trees to 4 m tall. Older (woody) stems irregularly fissured-striate, lenticellate, lacking trichomes; younger (herbaceous) stems quadrate-sulcate, glabrous (or with the surface roughened but lacking trichomes). Leaves seasonally deciduous, clustered at branch apices (and appearing quadrate at some nodes), petiolate, petioles 20–90 mm long, blades apparently subsucculent, lanceolate to ovate to elliptic, 82–260 mm long, 35–110 mm wide, 2–2.6 × longer than wide, (rounded to) acuminate at apex, cuneate to subattenuate at base, abaxial surface minutely glandular-punctate (sometimes not evident) and sparsely pubescent (especially near base) with flexuose eglandular trichomes 0.2–0.7 mm long or trichomes absent on mature leaves, adaxial surface very sparsely pubescent (if at all) with similar trichomes, margin entire to subsinuate, sparsely ciliate with trichomes like those of abaxial surface. Inflorescence a terminal sessile or pedunculate thyrse to 303 mm long (including peduncle, if present, and excluding corollas), peduncle (if present) to 52 (or more?) mm long, glandular-puberulent with glandular trichomes to 0.1 mm long, rachis pubescent with erect glandular trichomes 0.05–0.2 mm long; dichasia opposite, pedunculate, mostly 1–3-flowered, to 50 (–70 in fruit) mm long (excluding corollas), dichasial peduncles 6–14 (–29 in fruit) mm long, pubescent like rachis. Bracts caducous (not seen). Bracteoles caducous (not seen). Flowers pedicellate, pedicels 23–30 (–48 in fruit) mm long, pubescent like rachis. Calyx 5–9 mm long, lobes fused for 1–3.5 mm at base, subheteromorphic, apparently subsucculent, abaxially pubescent with erect to flexuose glandular trichomes 0.05–0.2 mm long, posterior lobe subconduplicate, broadly ovate to subtriangular, 3.5–4.5 mm long, 3–4.3 mm wide, sometimes smaller than lateral lobes, subacute to acute at apex, lateral lobes ovate to subtriangular, 4–4.8 mm long, 3–4 mm wide, acute at apex. Corolla green and maroon-purple, 35–39 mm long, externally puberulent with erect glandular trichomes to 0.1 mm long, tube 17–30 mm long, narrow proximal portion 4.5–9 mm long, 6–11 mm in diameter near midpoint, throat 11–20 mm long, 20–25 mm in diameter at mouth, lobes spreading to recurved, subtriangular to ovate, 10–13 mm long, 9–12 mm wide, rounded at apex. Stamens 4, 55–75 mm long, filaments glabrous (at least distally, proximal portion not seen), thecae 7.5–8 mm long; staminode (if present) not seen. Style 80–82 mm long, glabrous, stigma 2-lobed, lobes ± funnelform, 1.5 mm long, shape and width not determined. Capsule 38–47 mm long, 4.7–6 mm in diameter, pubescent throughout with erect glandular trichomes to 0.1 mm long, stipe 4 mm long. Seeds up to 24 per capsule, 4–4.5 mm long, 3–4 mm wide, surfaces minutely granulate to ± scurfy.

PHENOLOGY.— Flowering: January; fruiting: January–March. *Kruse 1380* noted that the flowers were “pronto caedizas,” possibly referring to their being soon deciduous during the day, and thus likely largely nocturnal.

DISTRIBUTION AND HABITAT.— Western Mexico (central Guerrero; Fig. 8); plants occur on limestone slopes in tropical subdeciduous forests (selva mediana subcaducifolia) at elevations near 750 m.

CONSERVATION.— Daniel (2017) discussed the rationale for and provided a preliminary conservation assessment of Data Deficient (DD) for *L. rzedowskianum*, which is known only from a single site.

ILLUSTRATIONS.— Rzedowski (1973:53, fig. 4).

DISCUSSION.— Daniel (2017) discussed the necessity for validating this name, its typification, and the sole collection locality.

ADDITIONAL SPECIMENS EXAMINED.— MEXICO. **Guerrero**: Mpio. Chilpancingo, Rincón de la Vía, cerca de Agua de Obispo, 9-VIII-1964 (vegetative) and 23-III-1963 (fruiting), *H. Kruse 1380* (EAP, ENCB, FCME, MEXU, MICH, MO, US); Mpio. Chilpancingo, Rincón de la Via, 27-I-1970, *H. Kruse 2701* [catalog # 4755] (MEXU); same locale, 14-VII-1970, *H. Kruse 2701-b* [catalog #5033] (B, FCME, MEXU).

11. ***Louteridium tamaulipense*** A. Richardson, *Sida* 3: 448. 1969. **Type**.— MEXICO. **Tamaulipas**: ca. 5 km NW of Gómez Farias toward Aguacates [ca. 23°03’47.94”N, 099°10’08.06”W], 370 m, rocky slope in wet forest, 30-VI-1969 (flr), *A. Richardson 1388* (holotype: TEX!, mounted on 4 sheets; isotypes: ENCB-image seen, F!, GH, K!, MEXU!, MICH!, NY!, OS-image seen, UC!, US!, WIS-images seen).

Perennial herbs to shrubs to 2.5 m tall, possibly epipetric (Richardson 1972:63). Older (woody) stems prostrate (fide Richardson 1972:70), subquadrate or becoming irregularly fissured, lacking trichomes; younger (herbaceous) stems quadrate-sulcate to quadrate-alate, glabrous. Leaves apparently not all seasonally deciduous, ± evenly dispersed along young stems, petiolate, petioles to 85 mm long, blades subsucculent, ovate to elliptic, 80–260 mm long, 22–115 mm wide, 1.9–4 × longer than wide, acuminate to subfalcate to caudate at apex, subattenuate to attenuate at base, surfaces glabrous, margin entire to subsinuate-crenate. Inflorescence a terminal pedunculate thyrse to 250 mm long (including peduncle and excluding corollas), peduncles to 84 mm long, evenly pubescent with erect to flexuose glandular trichomes 0.1–0.3 mm long, rachises similarly pubescent; dichasia sometimes modified by sympodial expansion and appearing as lateral branches (especially from proximal nodes of inflorescence), opposite, pedunculate, mostly 3–many-flowered, up to 115 mm long (excluding corollas), dichasial peduncles 3–45 mm long, pubescent like rachis. Bracts caducous, linear-lanceolate, 9–19 mm long, 1–2.3 mm wide, abaxially pubescent like rachis. Bracteoles and secondary bracteoles caducous, lanceolate to linear-lanceolate, 9–14 mm long, 2–3 mm wide, abaxially pubescent like rachis. Flowers pedicellate, pedicels to 46 mm long, pubescent like rachis. Calyx 32–47 mm long, lobes subheteromorphic, membranaceous in texture (i.e., neither succulent nor coriaceous), apically acuminate, abaxially pubescent like rachis, posterior lobe planar, lance-ovate to ovate, 33–45 mm long, 10–17 mm wide, slightly to conspicuously larger than other lobes, lateral lobes lance-ovate to ovate, 29–39 mm long, 8–14.5 mm wide. Corolla whitish to greenish yellow, 55–60 mm long, externally puberulent with scattered glands to 0.1 mm long, tube ca. 25–30 mm long, narrow proximal portion 3–6 mm long, 3–9 mm in diameter, throat 20–25 mm long, 20–30 mm diameter at mouth, lobes spreading to recurved, triangular to ovate, 15–27 mm long, 5.2–9 mm wide, tapered and ± acute at apex. Stamens 2, 50–63 mm long, filaments glabrous distally (not seen proximally), thecae 11–15 mm long; staminodes (if present) not seen. Style 48–73 mm long, glabrous distally, pubescent with glandular trichomes proximally, stigma unequally 2-lobed, lobes often recoiled, ± oblong, 1.5–3.5 mm long, width not determined. Capsule 22–28 mm long, diameter not determined, pubescent with glandular trichomes 0.05–0.2 mm long, stipe 1–4 mm long. Seeds up to 20 per capsule, 3.5–5 mm long, 3–4 mm wide, surfaces smooth or with low subconic tubercles.

Phenology.— Flowering: March–June, September, December; fruiting: March–April, September. Dressler (*s.n.*) notes that flowers are nocturnal. Richardson (1972) observed flowers of *L. tamaulipense* over 14 hours (from 18:00 to 08:00) in September of 1969. He noted: 1) that corollas began opening at sunset and falling in the early morning; 2) the lack of a floral scent; 3) that no nectar was found in the gibbous throat of corollas; 4) the nectary had an intensely sweet taste; and 5) hummingbirds visited flowers at dusk and in the early morning.

Distribution and habitat.— Northeastern Mexico (Tamaulipas; Fig. 8); plants occur on rocky limestone slopes in "tropical semi-evergreen and evergreen forest" (Richardson 1972) at elevations from 340 to 560 (to 1400) meters. The vegetation at collection sites has been characterized on specimen labels as wet forest, cloud forest, and "selva mediana subperennifolia."

Conservation.— *Louteridium tamaulipense* is a local endemic that is known in the vicinity of the Sierra de Guatemala (= Sierra de Cucharas) in the northern Sierra Madre Oriental of Tamaulipas, where its known distribution (EOO = 43 km^2) is confined to the Reserva de la Biosfera El Cielo. *Valiente B. et al. 285* noted that the species was locally very abundant. Several threats have been noted for the biosphere reserve, including: unplanned agricultural and forestry exploitation still being undertaken, overgrazing by livestock, increases in population density in surrounding buffer zones, poorly regulated eco-tourism, and poaching (Anonymous 2007). Most (or all?) of the collections have been made in the buffer zones outside of the two core areas (in which most human travel and exploitation are prohibited) of the reserve. The buffer zones, including the EOO, include roads, villages, and tourist facilities. However, historical landsat images (2005 to 2016) via Google Earth Pro (2018) reveal relatively little change in vegetation cover in the EOO. Thus, based on current knowledge of the species, it is not known to qualify for a threatened category in spite of its very small EOO. Based on the information summarized above, the species is provisionally assessed as Near Threatened (NT).

Discussion.— Richardson's (1972) observations on floral phenology and visitation are very similar to those noted above for *L. dendropilosum* in Oaxaca. *Louteridium tamaulipense* shows some similarities to *L. costaricense*, and can be distinguished from that species of southern Central America by characters in the following couplet:

1a. Corolla externally pubescent with glandular trichomes 0.1–0.5 mm long and eglandular trichomes 0.1–1 mm long, lower lip 13–22 mm long; capsule 27–35 mm long, glabrous, stipe 7–12 mm long; inflorescence peduncles, rachis, peduncles of dichasia, and abaxial surface of bracts and bracteoles glabrous (or the bracts and bracteoles sometimes glandular-punctate but lacking elongate trichomes); bracts and bracteoles persistent.. . . . . *L. costaricense*

1b. Corolla externally puberulent with glands to 0.1 mm long, lower lip 27–31 mm long; capsule 22–25 mm long, pubescent with glandular trichomes 0.05–0.2 mm long, stipe 1–4 mm long; inflorescence peduncles, rachis, peduncles of dichasia, and abaxial surface of bracts and bracteoles pubescent with glandular trichomes 0.1–0.3 mm long; bracts and bracteoles caducous . . . . *L. tamaulipense*

Additional specimens examined.— MEXICO. **Tamaulipas**: Mpio. Gómez Farías, 1 km SW de la Estación Canindo (sitio Cedros II), [ca. 23°02'23.25"N, 099°13'59.36"W], *L. Hernández 3022* (BRIT, QMEX); 8 km por la brecha W de Gómez Farías [ca. 23°02'43.51"N, 099°10'09.65"W], *E. Martínez S. et al. 3854* (ENCB, MEXU); ca. 5 km NW of Gómez Farías, *A. Richardson 1398* (K); Mpio. Gómez Farías, 1.5 km E de Gómez Farías, laderas de orientación WSW sobre la Sierra Chiquita [ca. 23°02'48.23"N, 099°08'26.35"W], *A. Valiente B. 490* (MEXU); Mpio Gómez Farías, 2 km W de Gómez Farías, postrimerias de la Sierra Madre Oriental, *A. Valiente B. et al. 285* (ARIZ, MEXU, RSA); Mpio. Gómez Farías, 1.5 km E de Gómez Farías, ladera de orientación W sobre la "Sierra Chiquita," *A. Valiente B. et al. 443* (MEXU). **Cultivated**: University of California Botanical Garden (acc. no. 60.889-1), grown from plants collected by R. Dressler (*s.n.*) in Tamaulipas, above Encino, on road to lumber camp Julillo [ca. 23°07'37.45"N, 099°09'45.46"W], *P. Hutchison 60-889-1* (UC).

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Appendix 1

Summaries of pollen measurements and information on sculptural elements for 10 species of *Louteridium* based on the collections indicated. Not all measurements could be made from all grains. n = number of grains measured, WD = widest grain diameter, AD = apertural diameter, larger sculptural element measurements = length × diameter, and smaller sculptural element measurement = diameter or longest axis parallel to exine surface. Shapes of sculptural elements are based on Walker and Doyle (1975).

L. brevicalyx (*Daniel & Steinmann 11913, Hinton et al. 15843, Reyes & Steinmann 5484,*). n = 4. WD = 106–132 µm; AD = 10–15 µm. Larger sculptural elements gemmate to baculate, 4–6 × 3–6 µm, smaller elements gemmate to baculate to pilate to rugulate or sometimes dense and nearly forming a reticulum, 0.1–1.4 µm.

L. chartaceum (*Daniel & Butterwick 5905*). n = 3. WD = 107–118 µm; AD = 7–18 µm. Larger sculptural elements gemmate to baculate, 3–7 × 4–6 µm, smaller elements verrucate, 0.3–2.5 µm.

L. costaricense (*van der Werff 7019*). n = 2. WD = 106-121 µm; AD = not clearly evident in samples. Larger elements gemmate, 4.0–5.7 × 4.3–6.3 µm, smaller elements gemmate to pilate, to baculate, 0.2–1.2 µm.

L. dendropilosum (*Daniel et al. 11784*, *Fernández N. 4189*). n = 3. WD = 114–131 µm; AP = 8–16 µm. Larger sculptural elements gemmate to baculate, 4.0–5.6 × 3.7–5.6 µm, smaller elements rugulate to verrucate, 0.5–0.8 µm.

L. donnell-smithii (*Breedlove & Almeda 57578*, *Daniel et al. 11356*, *Daniel & Véliz 11337*). n = 5. WD = 121–143 µm; AD = 7–10 µm. Larger sculptural elements gemmate, 2.2–6.1 × 3.4–6.1 µm, smaller elements echinate to rugulate, 0.4–0.9 µm.

L. mexicanum (*Foerther et al. 10940*, *Breedlove & Thorne 30786*, *Breedlove & Daniel 70879gh*). n = 3. WD = 117–141 µm; AD = 7–12 µm. Larger sculptural elements gemmate, 1.7–6.0 × 3.3–6.0 µm, smaller elements pilate to baculate, 0.3–1.0 µm.

L. parayi (*Daniel & Wendt 5805*, *Breedlove & Daniel 70889*). n = 3. WD = 130–132 µm; AD = 5–13 µm. Larger sculptural elements gemmate, 4–5 × 3–6 µm, smaller elements rugulate to verrucate, sometimes congested and nearly forming a reticulum, 0.5–1 µm.

L. purpusii (*Breedlove & Smith 31613*). n = 2. WD = 108–132 µm; AD = 11–18 µm. Larger sculptural elements gemmate, 4–6 × 4–6 µm, smaller elements rugulate to pilate, congested and nearly forming a reticulum, 1–2.5 µm.

L. rzedowskianum (*Kruse 1380*). n = 4. WD = 110–128 µm; AD = 5–13 µm. Larger sculptural elements baculate to gemmate, 4–5 × 3–4 µm, smaller elements gemmate, sometimes inconspicuous, scattered or nearly linked into a reticulum, 0.4–1.3 µm.

L. tamaulipense (*Hutchison 60-889-1*). n = 1. WD = 108 µm; AD = 7–9 µm. Larger sculptural elements gemmate, 3–5 × 4 µm, smaller elements rugulate, congested and nearly forming a reticulum, 0.3–1.3 µm.

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Heterobranch Sea Slug Range Shifts in the Northeast Pacific Ocean associated with the 2015-16 El Niño

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The strong 2015–16 El Niño comprised the second part of the unprecedented 2014–17 marine heat wave in the Northeast Pacific Ocean. From late 2015 through 2017 we sampled mostly intertidal sites from La Paz, Baja California Sur to northern Oregon for benthic heterobranch sea slugs outside of their normal ranges. Combined with records obtained from colleagues and internet sources, we document northern range shifts for 37 species, including 21 (*Berthella strongi, Okenia angelensis, Acanthodoris rhodoceras, Crimora coneja, Limacia mcdonaldi, Polycera atra, Triopha maculata, Carminodoris bramale*, *Doris* cf. *pickensi*, *Thordisa rubescens*, *Cadlina sparsa, Doriopsilla albopunctata, Doriopsilla fulva, Doriopsilla gemela, Tritonia myrakeenae, Doto lancei*, *Doto* form A of Goddard (1996), *Flabellina bertschi, Hermosita hakunamatata, Noumeaella rubrofasciata, Phidiana hiltoni*) from new northernmost localities. The average range extension of these 21, plus *Hermissenda opalescens* and *Dirona picta* reported by Merlo et al. (2018) from the west coast of Vancouver Island was 270 km (SD = 201 km, n = 23). Significantly, no species were observed south of their usual ranges during the 2014–17 marine heat wave. Combined with the results of Goddard et al. (2016) for the 2014 warm anomaly, the 2014-17 marine heat wave in the Northeast Pacific drove range shifts in at least 52 species of benthic heterobranchs, approximately one quarter of the species known from the region. These numbers appear to be unprecedented in the historical record and point to global warming as a contributing factor, likely acting through a series of steps leading to increased poleward transport of coastal waters in the region, as well as elevated sea-surface temperatures.

KEYWORDS: Range shifts, heterobranch sea slugs, nudibranchs, Northeast Pacific Ocean, marine heat wave, El Niño, global warming

INTRODUCTION

The 2015-16 El Niño in the tropical Pacific was one of the strongest on record. However, its physical effects on the California Current System, including coastal waters, were weaker than expected (Jacox et al. 2016). This resulted in part because as the El Niño formed, the entire northeast Pacific was already in the midst of a multi-year marine heat wave of unprecedented magnitude (Bond et al. 2015; Di Lorenzo and Mantua 2016), causing extensive biological impacts at all trophic levels and poleward range shifts typically observed only during strong El Niño events (reviewed by Cavole et al. 2016; and see Jones et al. 2018). The range shifts driven by the 2014-15 warm anomaly included 30 species of heterobranch sea slugs (heterobranchs), nine of which were found in new northernmost localities (Goddard et al. 2016). During the 2015-16 El Niño, Merlo et al. (2018) found *Hermissenda opalescens*, which was separated by Lindsay and Valdés (2016) from its more northerly pseudocryptic sister *H. crassicornis*, on the west coast of Vancouver Island, British Columbia. Merlo et al. (2018) also reported *Dirona picta* for the first time north of Oregon. Here, we document additional range extensions of northeast Pacific heterobranchs associated with the 2015-16 El Niño and the warm water anomaly that persisted into 2017 in the northern California Current System (Well et al. 2017) and summarize the effects of the combined warm water events (hereafter the 2014-17 marine heat wave) on the distribution of heterobranchs in the region.

METHODS AND STUDY SITES

From fall 2015 through 2017, we sampled for benthic heterobranchs at mostly intertidal sites from Baja California Sur, Mexico to Oregon (Table 1), including many of the same sites sampled annually to quarterly by Goddard et al. (2016) using timed counts. We photographed living specimens in the field or laboratory. A few were collected and deposited in the Invertebrate Zoology Collection at the California Academy of Science (CAS) as voucher specimens and are referenced below by their CASIZ catalog numbers, records of which can be accessed online via the CAS Invertebrate Zoology Collection Database <*http://researcharchive.calacademy.org/research/izg/iz_coll_db/index.asp*>. We were also sent new records of occurrence by colleagues, particularly in Washington and British Columbia, and we also monitored citizen science posts on websites such as iNaturalist, OCDiving, and Flickr for sightings of heterobranchs beyond their usual ranges. From both of these latter types of sources we include below only records accompanied by an image and the date and locality of observation.

We calculated the range shift for each species by using the Ruler tool on Google Earth to measure the straight-line distance between the previous northernmost known locality and its new northernmost locality documented below. This measure is conservative and actually measures range extensions, because it is based on the distance between recorded northernmost localities, typically reached during strong El Niño events, rather than the distance between the new northernmost locality and a species' usual northern range limit. However, information on the latter has not actually been compiled, and is spotty, scattered throughout a wide range of sources, and for many species qualitative in nature.

Nomenclature used below follows the World Register of Marine Species (WoRMS) <*http://www.marinespecies.org/index.php*>, as of June 2018.

RESULTS

Including *Hermissenda opalescens* and *Dirona picta*, whose ranges were extended by Merlo et al. (2018), 23 species of heterobranchs were recorded from new northernmost localities from late

TABLE 1. Names and geographic coordinates of recent collecting sites from British Columbia (BC, Canada), Washington (WA), Oregon (OR), California (CA), and Baja California Sur (BCS). All sites intertidal unless noted otherwise.

Site	Latitude, Longitude
Bear Cove, Port Hardy, Vancouver Is., BC, Canada (subtidal)	50.7222° -127.4597°
Monas Is., Lemmens Inlet, Clayoquot Sound, Vancouver Is., BC (oyster racks)	49.1904° -124.8859°
East end of Stockham Island, Clayoquot Sound, Vancouver Is., BC (kelp bed)	49.1692° -125.8937°
Chibahdehl Rocks, Cape Flattery, WA (subtidal)	48.3942° -124.6774°
Haystack Rock, Cannon Beach, OR	45.8844° -123.9670°
Oceanside Beach State Park, OR	45.4619° -123.9729°
Netarts Bay, OR (subtidal)	45.4301° -123.9456°
South side Netarts jetty, Netarts Bay, OR	45.4293° -123.9476°
South side of Boiler Bay, OR	44.8289° -124.0634°
Otter Crest, OR	44.7529° -124.0656°
Yaquina Bay, OR	44.6246° -124.0433°
Seal Rock State Wayside, OR	44.4918° -124.0861°
Yachats, OR	44.3138° -124.1095°
Neptune State Scenic Viewpoint, OR	44.2634° -124.1101°
Strawberry Hill, OR	44.2509° -124.1143°
Bob Creek, OR	44.2423° -124.1127°
Gregory Point, OR	43.3400° -124.3749°
Cape Arago, OR	
North Cove	43.3094° -124.3986°
Middle Cove	43.3026° -124.4007°
South Cove	43.3026° -124.3988°
Crook Point, OR	42.2511° -124.4136°
Whiskey Creek, OR	42.2227° -124.3830°
House Rock, OR	42.1130° -124.3550°
Lone Ranch, OR	42.0997° -124.3493°
Palmer’s Point, CA	41.1319° -124.1642°
Woodley Island, Humboldt Bay, CA	40.8077° -124.1666°
MacKerricker State Park, CA	39.4907° -123.8035°
Glass Beach, CA	39.4533° -123.8143°
Moat Creek, CA	38.8794° -123.6809°
Salt Point State Park, CA	38.5648° -123.3332°
Coleman Beach, CA	38.3632° -123.0708°
Miwok Beach, CA	38.3612° -123.0701°
Pinnacle Rock, CA	38.3050° -123.0172°
Dillon Beach, CA	38.2538° -122.9695°
Drake’s Estero, CA	38.0351° -122.9279°
Duxbury Reef, CA	37.8903° -122.6998°
Elkhorn Slough, CA	36.8090° -121.7849°
Monterey Breakwater, CA (subtidal)	36.6085° -121.8905°
Carmel Point, CA	36.5435° -121.9342°
Point Sierra Nevada, CA	35.7130° -121.3167°
Estero Bluffs State Park, CA	35.4464° -120.9440°
T pier, Morro Bay, CA (subtidal)	35.3694° -120.8559°
Morro Bay, CA	35.3440° -120.8448°
Hazard Canyon Reef, CA	35.2897° -120.8844°
Point Buchon, CA	35.2551° -120.8996°
Cave Landing, CA	35.1752° -120.7223°
Tarantula Reef, CA	34.4952° -120.4972°
Gaviota, CA	34.4686° -120.2373°
Naples, CA	34.4337° -119.9501°
Ellwood Mesa Reef, CA (subtidal)	34.4177° -119.9015°
Northeast Santa Cruz Island, CA (subtidal)	34.0449° -119.6015°
Anacapa Island, CA (subtidal)	
N side, East Anacapa Is.	34.0175° -119.3667°
Pelican Preserve, West Anacapa Is.	34.0121° -119.4157°
S side, West Anacapa Is.	34.0079° -119.4381°
Dana Point Harbor, California (docks)	33.4605° -117.7069°
Mission Bay, San Diego, CA (subtidal)	32.7617° -117.2466°
Punta Entrada, Isla Magdalena, Bahía de Magdalena, BCS (subtidal)	24.5443° -112.0588°
Playa Pichilingue, La Paz, BCS	24.2854° -110.3283°

2015 through 2017 and are listed systematically in Section 1 below. For each of these we include their known southern range limit and previous northern range limit, along with the primary references documenting those. We also include, as "additional northern localities," records from sites located between the new and previous northernmost localities; for a few species these also include older, previously undocumented or obscure records.

New northernmost sites were spread over 26 degrees of latitude, from La Paz, Baja California Sur (for *Carminodoris bramale*) to Port Hardy, Vancouver Island, British Columbia (for *Triopha maculata*). Range extensions varied in length from 23 to 700 km, with a mean of 270 km (SD = 201 km, n = 23).

Section 2 covers species found at or near previously determined northern range limits.

Each of the recent collecting localities mentioned below is listed with its geographic coordinates in Table 1.

I. New northernmost locality records

Heterobranchia

Pleurobranchida

Berthella strongi (MacFarland, 1966). MacKerricker State Park, Mendocino Co., California, 1 specimen, low rocky intertidal, 4 July 2016 (Pirrone 2016) to El Tomatal, Baja California, Mexico (Goddard and Green 2013; for image see <*https://www.inaturalist.org/observations/2957040*>).

Previous northernmost locality: Moss Beach, California (Bertsch et al. 1972 [as *Pleurobranchus strongi*]).

Additional northern localities: Salt Point State Park, Sonoma Co., California, 1 specimen, low intertidal, 9 May 2016 (observed by WP, DM, PD); Drake's Estero, Point Reyes National Park, Marin Co., California, 1 specimen, with an egg mass, next to its sponge prey *Oscarella carmela*, under a low intertidal cobble, 8 June 2016 (observed by JG).

Remarks: Behrens (1998, 2004) reported *B. strongi* found by Mike Miller off of Nanaimo, British Columbia. No collection information, including date, or image were given, but M. Miller (personal communication to JG, 9 July 2016) dove there in 1998, and the record therefore may represent an ephemeral range extension driven by the strong 1997-98 El Niño event. However, it should be noted that this species has not been reported from north of California before or since, and without an image or specific collection data we consider this record unverified.

Nudibranchia

Goniodorididae

Okenia angelensis Lance, 1966. Miwok Beach, Sonoma Co., California, 1 specimen, 5 mm long, low rocky intertidal, 27 May 2017, observed by Colby Davidson (Fig. 1A) (Hollis Bewley, personal communication to JS, 5 June 2017) to Punta Rosarito, Baja California, Mexico (Goddard and Hermosillo 2008); Bahía de los Ángeles, Baja California (Lance 1966) and Chile (Muñoz et al. 1996; Schrödl 1996).

Previous northernmost locality: San Francisco Bay, California (Lance 1966).

Remarks: The new record is also significant for its location on the outer coast, outside the seasonal warm water refugium of San Francisco Bay.

Onchidorididae

Acanthodoris rhodoceras Cockerell in Cockerell and Eliot, 1905. Chup Point, Barkley Sound, Vancouver Island, British Columbia, 1 specimen, 12 m depth, 21 May 2018 (Fig. 1B) found by Kathy Johnson (P. Mieras, personal communication to JG, 2 June 2018) to Bahía Tortugas, Baja California, Mexico (Behrens 1991) and Bahía de los Ángeles, Baja California (Bertsch 2014).

Previous northernmost locality: South side of Netarts Jetty in Netarts Bay, Oregon, 1 specimen 12 mm long, low intertidal, 17 June 2015 (observed by TP; see Maginnis 2016).

Remarks: The identity of specimens collected in the 1960s from Alaska (including the Arctic Ocean) and Vancouver Island by J. McLean, and referred to as *A. rhodoceras* by Fahey and Valdés (2005), needs to be verified for the following reasons. First, except for the specimen recently found in Barkley Sound, there are no other records of *A. rhodoceras* from north of Oregon, including from Bernard (1970), Millen (1983, 1989), Lee and Foster (1985), Goddard et al. (1997), Goddard and Foster (2002), Lamb and Hanby (2005), and Fletcher (2013). Second, no other heterobranch gastropod is known to have a geographic distribution extending from the Arctic Ocean into the Gulf of California (see Behrens and Hermosillo 2005), especially as recent integrative systematic studies have shown that nudibranchs from the Northeast Pacific Ocean once considered to have broad geographic ranges are actually complexes of species with more limited, but overlapping ranges (e.g., Lindsay et al. 2016; Lindsay and Valdés 2016). Based on the records of *A. pilosa* (Abildgaard, 1789) and the closely related *A. atrogriseata* O'Donoghue, 1927 from the North Pacific, including the Aleutian Islands and south central Alaska (Lee and Foster 1985; Hallas et al. 2016), we think it likely the specimens collected by McLean in Alaska are either one or both of those species, a result likely to influence the biogeographic analyses conducted by Hallas et al. (2016), who relied on the distribution information given by Fahey and Valdés (2005) for *A. rhodoceras*, and who incorrectly showed it in their Figure 3 as being the only species of *Acanthodoris* present along most of the Pacific coast of Alaska.

Polyceridae

Crimora coneja Er. Marcus, 1961. Boiler Bay, Lincoln Co., Oregon, 29 April 2017, 2 specimens, low rocky intertidal at south end of bay, observed by Lillian Mayer and her Biology class from Clackamas Community College (L. Mayer, personal communication to JG, 1 May 2017; for image see Nosler 2017) to Point Loma, San Diego, California (Marcus 1961).

Previous northernmost locality: North Cove, Cape Arago, Oregon (Goddard 1984).

Limacia mcdonaldi Uribe, Sepúlveda, Goddard and Valdés, 2017. Moat Creek Beach, Mendocino Co., California, 24 June 2017, 1 specimen, low rocky intertidal (observed by JG; for image see <*https://www.inaturalist.org/observations/6868719*>) to Cabo San Lucas (Lance 1961) and into the Gulf of California to Bahía de los Ángeles (Keen 1971; Angulo-Campillo 2003, 2005).

Previous northernmost locality: Not clear, owing to identification until 2017 as *L. cockerelli* (MacFarland, 1905). Images show that *L. mcdonaldi* has occurred on the Monterey Peninsula since at least the 1960s and 70s (e.g., McDonald 2016; Goddard 2017a). Since 2014 *L. mcdonaldi* has also been recorded many times from San Mateo and Marin counties (RA, personal observations; and see <*https://www.inaturalist.org/observations?verifiable=true&taxon_id=538831&place_id=&preferred_place_id=&locale=en*>).

Additional northern localities: Salt Point State Park, Sonoma Co., California, 9 May 2016, 1 specimen, low rocky intertidal (observed by WP, DM, PD). Drake's Estero, Point Reyes National Seashore, California, 15 specimens, low rocky intertidal shelf just inside mouth of the estero, 8 June 2016 (observed by JG; for image see <*https://www.inaturalist.org/observations/5397011*>).

Polycera atra MacFarland, 1905. Monas Island, Lemmens Inlet, Meares Island, Clayoquot Sound, Vancouver Island, British Columbia, several specimens on suspended oyster culture array next to Monas Island, July and August 2015 (Fig. 1C) (A. Murray, personal communication to JG, 26 April 2017) to Punta Pericos, Baja California Sur (Angulo-Campillo 2003, 2005).

Previous northernmost locality: Westport, Grays Harbor, Washington (Lamb and Hanby 2005; and see Goddard et al. 2016).

Additional localities in Oregon: Seal Rock, 8 May 2016, 1 specimen (observed by TP); Neptune State Scenic Viewpoint, 20 May 2015, 1 specimen (TP); Strawberry Hill, 8 April 2016, 1 specimen (TP).

Triopha maculata MacFarland, 1905. Bear Cove, Port Hardy, Vancouver Island, British Columbia, 19 total specimens, with 7 egg masses, 3-12 m depth, September to October 2015, observed and photographed by Jackie Hildering, plus 1 specimen, 4 m depth, 22 October 2016, observed and photographed by Alexandra Spicer (records listed by Pacific Northwest Shell Club 2016) to Punta Rosarito, Baja California (Goddard and Schickel 2000).

Previous northernmost locality: Bamfield, Vancouver Island, British Columbia (Millen 1983).

Additional northern localities: Entrance of Lemmens Inlet, Clayoquot Sound, Vancouver Island, British Columbia, many specimens with egg masses on *Macrocystis pyrifera* adjacent to the east end of Stockham Island, August - October 2015 (A. Murray, personal communication, with images, to JG, 22 March 2016).

Remarks: Jackie Hildering, an experienced underwater naturalist and observer of nudibranchs, reported (personal communication to JG, 16 March 2016) that in approximately 150 dives over 15 years in the Port Hardy area, she had not observed *T. maculata* before September 2015.

Discodorididae

Carminodoris bramale (Fahey and Gosliner, 2003). Playa Pichilingue, La Paz, Baja California Sur, Mexico, 12 specimens, up to 75 mm long, with egg ribbons, on and near encrusting yellow sponge on the underside of low intertidal cobbles in the outlet of the lagoon behind the playa, 27 December 2017 (observed by JG; for images see: <*https://www.inaturalist.org/observations/9332510*>) to Isla de Coiba, Panama (Hermosillo 2004 [as *Hoplodoris bramale*]).

Previous northernmost locality: La Cruz de Huanacaxtle, Bahía de Banderas, Mexico (Hermosillo 2006).

Remarks: The specimens from La Paz are the first record of *C. bramale* from the Gulf of California and the Baja California peninsula. It was not recorded by Angulo-Campillo (2005) during his four year survey of opisthobranchs from Baja California Sur, including the La Paz area.

Thordisa rubescens Behrens and Henderson, 1981. Northeast Santa Cruz Island, California, 1 specimen, 15 m depth, 1 November 2017 (Figure 1D), observed by David Kushner, Kenan Chan, and Joshua Sprague (D. Kushner, personal communication to JG, 13 November 2017) to Punta Eugenia, Baja California Sur (Bertsch et al. 2000).

Previous northernmost locality: Paradise Cove, Malibu, Los Angeles Co., California (Behrens and Henderson, 1981).

Remarks: The specimen from Santa Cruz Island appeared to be dull orange to rust colored, but had the distinctive “halos” of lighter pigment around the rhinophores and gill plume described by Behrens and Henderson (1981) for this species (Figure 1D).

Few specimens of this Californian species have been found since its original description (Behrens 2016), so it is noteworthy that “dozens” have been observed, including some mating and

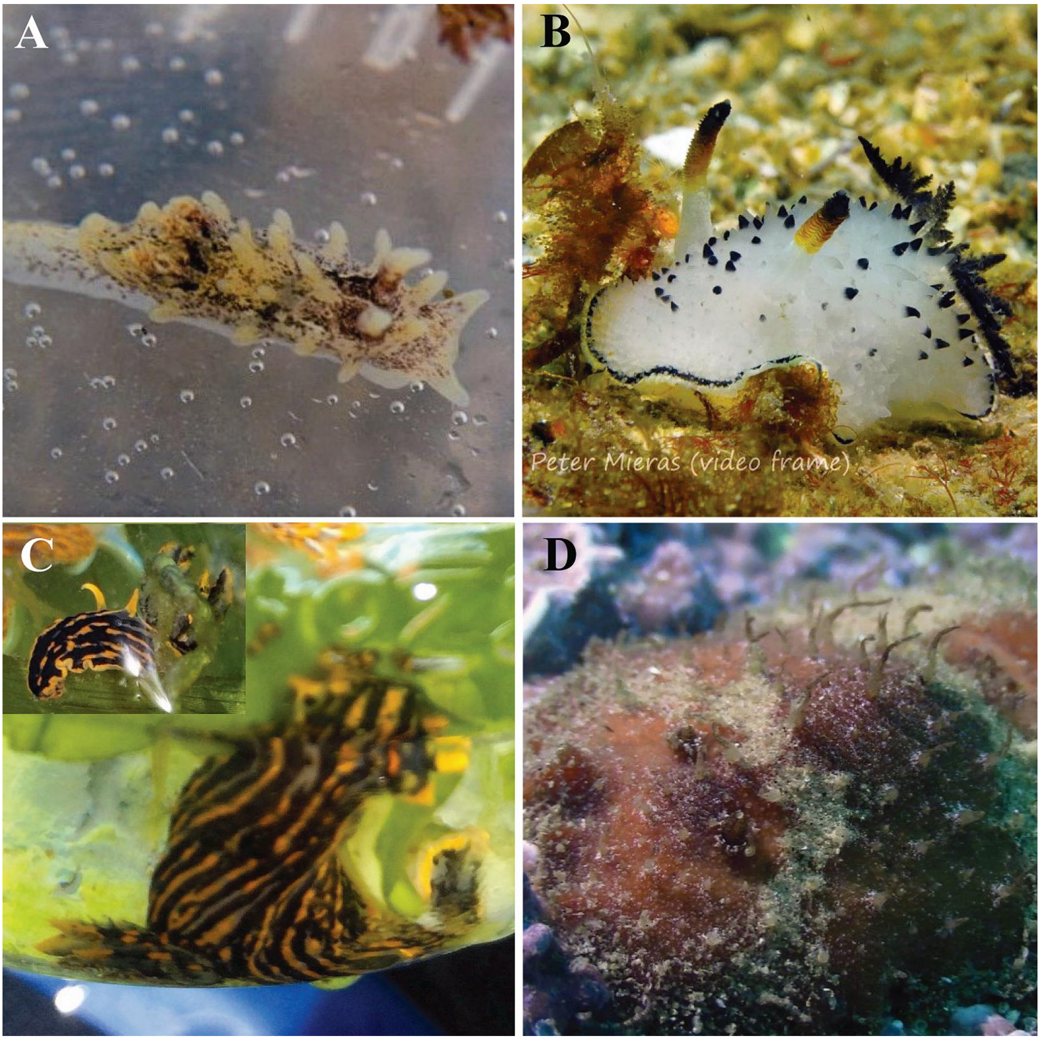

FIGURE 1. Heterobranch sea slugs found at new northernmost localities in the Northeastern Pacific Ocean, 2015–2017. **A** *Okenia angelensis*, Miwok Beach, Sonoma Co., California, 27 May 2017. Image by Colby Davidson. **B** *Acanthodoris rhodoceras*, Chup Point, Barkley Sound, Vancouver Island, British Columbia, 21 May 2018. Image by Peter Mieras/subvisionproductions.com. **C** *Polycera atra*, Lemmens Inlet, Clayoquot Sound, Vancouver Island, British Columbia, 25 July 2015. Inset: tail. Images by Brandon Exner. **D** *Thordisa rubescens*, Santa Cruz Island, California, 1 November 2017. Image by Kenan Chan/Channel Islands National Park.

laying eggs, the past two years on subtidal reefs around the Palos Verdes Peninsula (P. Garner, personal communication to RA, 20 June 2018; and see <*https://www.inaturalist.org/taxa/50139-Thordisa-rubescens*>).

Although Behrens and Henderson (1981) reported finding one specimen off the Palos Verdes Peninsula, the other three specimens they listed all came from "Big Kelp Reef, Paradise Cove, Los Angeles Co.," and the geographic coordinates they gave for that site place it in Malibu, not Palos Verdes as implied in Behrens and Hermosillo (2005).

Dorididae

Doris* cf. *pickensi Ev. Marcus and Er. Marcus, 1967. Morro Bay, San Luis Obispo Co., California, 7 specimens, on encrusting yellow sponge, 4 m depth near T Pier, 25 May 2016 (Fig. 2A) (observed by CH) to La Jolla, California (observed by JG, CASIZ 186472); northern Gulf of California (Marcus and Marcus 1967) to Costa Rica (Camacho-García et al. 2005).

Previous northernmost locality: Naples, Santa Barbara Co., California (Goddard and Green 2013; Goddard 2017).

Remarks: A specimen found by CH in Morro Bay laid a flat egg ribbon identical to that described by Goddard and Green (2013, p. 57) for this species from Santa Barbara County.

With their uniform yellow coloration and lack of dark pigmentation, up to 15 unipinnate gills, low rounded spiculate dorsal papillae, triangular labial tentacles, and hamate radular teeth (for images see Goddard 2017b), specimens of this species from California differ from all other yellow dorid nudibranchs known from the Northeast Pacific Ocean and may be undescribed. They are closest to *Doris pickensi* originally described by Marcus and Marcus (1967) and redescribed by Camacho-García and Gosliner (2008), but need to be fully compared – including with molecular genetics – with specimens from the vicinity of the type locality of that species at Puerto Peñasco in the northern Gulf of California to resolve their identity.

Cadlinidae

Cadlina sparsa (Odhner, 1921) Drakes' Estero, Point Reyes National Seashore, California, 3 specimens, low rocky intertidal, 8 June 2016 (observed by JG; for image see <*http://www.inaturalist.org/observations/5855244*>) to Punta Rosarito, Baja California, Mexico (JG, personal observations, 28 May 2001); Bahía de Banderas to Panama (Hermosillo 2004, Table 2; Hermosillo et al. 2006); Chile and Argentina (Marcus 1959; Schrödl 2000).

Previous northernmost locality: Marin Co. headlands, California (Jaeckle 1983).

Additional northern localities: Duxbury Reef, California, 1 specimen, 21 December 1992 (CASIZ 66769), 1 specimen, 23 December 2011 (JG, personal observations).

Dendrodorididae

Doriopsilla albopunctata (Cooper, 1863). Whiskey Creek, Curry Co., Oregon, 1 specimen, low rocky intertidal, 29 May 2017 (Fig. 2B) (observed by NT) to San Diego, California and possibly Baja California (Hoover et al. 2015).

Previous northernmost locality: not clear, owing to inclusion of *D. fulva* as a junior synonym of *D. albopunctata* until publication of Hoover et al. (2015). The latter authors give Mendocino, California as the northern range limit of *D. albopunctata*.

Additional northern localities: Palmer's Point, Patrick's Point State Park, California, 2 specimens, low rocky intertidal, 7 June 2016 (observed by JG). Glass Beach, Fort Bragg, California, 1 specimen, low rocky intertidal, 23 June 2017 (observed by JG; for image see <*https://www.inaturalist.org/observations/6872674*>).

Doriopsilla fulva (MacFarland, 1905). Netarts Bay, Oregon, at least 14 total specimens, rock rubble, 4–8 m depth, April, June, July, August 2016, June 2017 (Fig 2C) (Todd Cliff, personal communications to JG, 18 December 2016 and 25 June 2017) to Laguna Guerrero Negro, Baja California, Mexico (Bertsch and Aguilar Rosas 2016).

Previous northernmost locality: Whiskey Creek, Curry Co., Oregon (Goddard et al. 2016).

Additional northern localities: Middle Cove, Cape Arago, Oregon, low rocky intertidal, 3 specimens (CASIZ 216866, 209506, 209501), 5 June 2016 (observed by JG and NT; for image see <*http://www.inaturalist.org/observations/3528069*>); 1 specimen, 27 May 2017 (observed by NT). Crook Point, Curry Co., Oregon, 2 specimens, low rocky intertidal, 7 February 2016 (observed by NT).

Remarks: Goddard et al. (2016) reported finding a single juvenile *D. fulva* at Whiskey Creek, Oregon in June 2015, the first specimen of this species reported from north of California. One year later (6 June 2016) at the same site JG and NT counted 43 specimens of *D. fulva*, and a year after that (29 May 2017) NT found 11 specimens. For the southern Oregon coast as a whole, only two specimens of *D. fulva* were found in 2015 (Goddard et al. 2016). This was based on 37 trips to 20 sites, largely by NT. The following year NT counted a total of 204 individuals in 19 visits to 13 of those same sites, finding *D. fulva* at seven of them. Through the first half of 2017 NT had counted 24 total individuals of *D. fulva* at four out of 10 sites visited in southern Oregon. Todd Cliff and Andy Lamb found at least 5 specimens in Netarts Bay on 5 June 2017 (Todd Cliff, personal communication to JG, 25 June 2017).

Doriopsilla gemela Gosliner, Schaefer and Millen, 1999. Elkhorn Slough, Moss Landing, California, 1 specimen, 4 m depth, just inside entrance to slough, 5 July 2016 (Bentall 2016) to Bahía Tortugas, Baja California Sur (Bertsch and Aguilar Rosas (2016).

Previous northernmost locality: Monterey, California (Hoover et al. 2015; Goddard et al. 2016; and see <*https://www.inaturalist.org/observations/5220737*>).

Additional northern localities: T Pier, Morro Bay, California, 19 specimens with egg masses on shell rubble, 3–4 m depth, 25 May 2016 (observed by CH).

Tritonidae

Tritonia myrakeenae Bertsch and Mozqueira, 1986. Estero Bluffs State Park, San Luis Obispo Co., California, 3 specimens, among the octocoral *Clavularia* sp. under low intertidal cobbles, 29 April 2017 (observed by JG; for image see <*https://www.inaturalist.org/observations/6358562*>) to Costa Rica and Panama (Camacho-García et al. 2005).

Previous northernmost locality: Santa Barbara, California (Behrens 1980).

Additional northern localities: Cave Landing, San Luis Obispo Co., 4 specimens, 27 May 2013; 1 specimen, 8 October 2014; 1 specimen, 9 March 2016 (observed by JG); Tarantula Reef, Jalama Beach, Santa Barbara Co., 1 specimen, 5 July 2012; 1 specimen, 2 February 2015 (observed by JG); Gaviota, Santa Barbara Co., 6 specimens, 7 May 2012 (observed by JG); Naples, Santa Barbara Co., 1186 specimens, October 2006 – April 2017 (observed by JG).

Remarks: This diminutive tritonid, which has been by far the most abundant nudibranch at Naples, is usually found associated with the stoloniferous octocoral *Clavularia* sp., on whose polyps it preys (for image see <*https://www.inaturalist.org/observations/5396758*>).

Dotoidae

Doto lancei Ev. Marcus and Er. Marcus, 1967. Dana Point Harbor, California, 1 specimen, 18 November 2017 (Stacey 2017) to Panama (Hermosillo 2004).

Previous northernmost locality: Mission Bay, San Diego, California (Behrens 1991).

Remarks: Behrens (2004) reported *D. lancei* from Monterey Bay, but without an image to confirm the identification, we suspect it was actually *D. columbiana* O'Donoghue, 1921, which is common in central and northern California and superficially resembles light colored *D. lancei* but has shorter ceratal tubercles lacking the apical spots characteristic of *D. lancei*.

***Doto* form A** of Goddard (1996). Woodley Island, Humboldt Bay, Humboldt Co., California, 1 specimen on side of floating dock, 20 May 2016 (Young 2016) to Punta Rosarito, Baja California (JG, personal observations) and probably Baja California Sur (Angulo-Campillo 2005 [as *D. amyra*]).

Previous northernmost locality: Drake's Estero, Point Reyes National Seashore (Goddard 1996).

Additional northern localities: Coleman Beach, Sonoma Co., California, 2 specimens, low rocky intertidal, 26 June 2017 (observed by JG; for image see <*https://www.inaturalist.org/observations/6847120*>).

Remarks: This form is often identified as *Doto amyra*, but differs from that species in morphology, egg size, mode of development, and genetics (see Goddard et al. 2016, p. 29).

Dironidae

Dirona picta MacFarland in Cockerell and Eliot, 1905. Barkley Sound, Vancouver Island, British Columbia, at least 1 specimen, summer 2016 (Merlo et al. 2018; C. Tamis, personal communication to JG, with images, 12 June 2018) to Baja California Sur, and northern Gulf of California (Farmer and Collier 1963; and see CASIZ Collection database).

Previous northernmost locality: Cape Meares, Oregon (Goddard 1997).

Additional northern localities: Seal Rock State Wayside, Oregon, low rocky intertidal, 2 total specimens, 7 June and 3 July 2016 (observed by TP).

Flabellinidae

Flabellina bertschi Gosliner and Kuzirian, 1990. Anacapa Island, California, 1 specimen, 12 m depth, South side of West Anacapa Is., 26 Aug 2016 (Klug 2016a) to Panama (Hermosillo 2004).

Previous northernmost locality: Big Fisherman's Cove, Santa Catalina Island (Goddard et al. 2016).

Additional northern localities: Mission Bay Point, San Diego, California, 1 specimen, 2 m depth, rock rubble, 20 May 2016 (observed by CH). Mission Bay Drive bridge, San Diego, California, at least 24 specimens on pier pilings, maximum depth 5 m, 21 November 2016 (observed by BG; for image see <h*ttps://www.inaturalist.org/observations/4632067*>).

Facelinidae

Hermissenda opalescens (Cooper, 1863). Yellow Bank, Clayoquot Sound, Vancouver Island, British Columbia, 24 specimens, 15 July 2016 (Merlo et al. 2018) to Baja California Sur (Angulo-Campillo 2005); northern Gulf of California, Mexico (Farmer and Collier, 1963; Keen 1971).

Previous northernmost locality: Charleston, Oregon (Goddard 1984 [as *H. crassicornis*, form lacking bluish-white stripe on cerata; see remarks below])

Additional northern localities: 7 localities in Barkley Sound, Vancouver Island, British Columbia, summer 2016 (Merlo et al. 2018), Cape Flattery, Washington (Chibahdehl Rocks, Box Canyon, Steve's Cave), August 2015 (Fig. 2D) (K. Fletcher, personal communication with images to JG, 26 April 2016), Haystack Rock, Cannon Beach (Cullin 2017), Oceanside Beach State Park (observed by TP, 24 April 2016), Otter Crest (observed by TP, June to July 2016), Seal Rock (observed by TP, May to July 2016), Strawberry Hill (observed by TP, April to July 2016 and JG, 4 June 2016; for image see <*http://www.inaturalist.org/observations/3527960*>), Bob Creek (observed by TP, 7 May and 5 July 2016). Additional records of *H. opalescens* from Oregon in 2016 and 2017 are available on iNaturalist (<*http://www.inaturalist.org/taxa/494603-Hermissenda-opalescens*>).

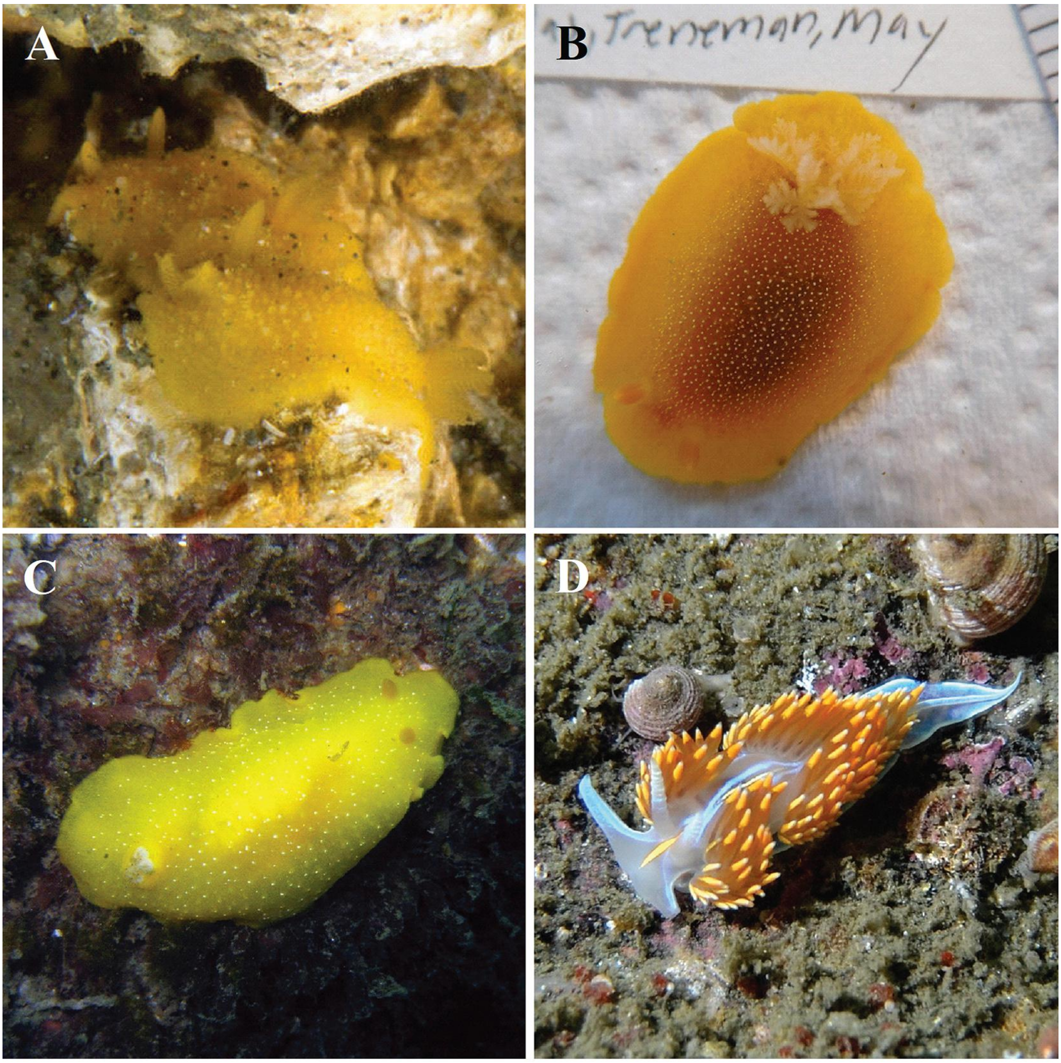

FIGURE 2. Nudibranch sea slugs found at new northern localities in the Northeastern Pacific Ocean, 2015–2017. **A** *Doris* cf. *pickensi*, Morro Bay, California, 25 May 2016. Image by CH. **B** *Doriopsilla albopunctata*, Whiskey Creek, Curry Co., Oregon, 19 May 2017. Image by NT. **C** *Doriopsilla fulva*, Netarts Bay, Oregon, 16 July 2016. Image by Todd Cliff. **D** *Hermissenda opalescens*, Box Canyon, Neah Bay, Washington, 20 August 2015. Image by Doug Miller.

Remarks: Lindsay and Valdés (2016) reinstated *H. opalescens* as distinct from *H. crassicornis* (Eschscholtz, 1831) and showed that externally *H. opalescens* can be distinguished in the Northeast Pacific Ocean from *H. crassicornis* by the lack of white stripes on the cerata of the former. The two color forms have long been recognized in field guides to nudibranchs from the northeastern Pacific Ocean (e.g., Behrens 1980; McDonald and Nybakken 1980). Lindsay and Valdés (2016, pp. 7 and 8) described the range of *H. opalescens* as extending from "the Sea of Cortez through Oregon," but in their conclusions described *H. opalescens* as ranging north only to Bodega Bay, apparently using a more conservative standard based solely on specimens they sequenced. They then stated that *H. crassicornis* and *H. opalescens* overlap in range "between Point Reyes and

Bodega Bay," a distance of only a few km. However, based on the presence or absence of the ceratal stripes, images by Bruce Wight available on the Sea Slug Forum <*http://www.seaslugforum.net/showall/hermcras*> show that *H. crassicornis* has been known since at least 2000 from as far south as San Miguel Island, California. Further, Goddard (1984, 1987, 1990), citing Behrens (1980), noted directly or indirectly the presence of non-striped *Hermissenda* (what we now know to be *H. opalescens*) at Charleston, Cape Arago, and Humbug Mountain, Oregon, and Punta Gorda in northern California. He found few *H. opalescens* relative to the numbers of *H. crassicornis* at these sites, and their occurrence was probably associated with the El Niño events of 1982-83 and 1986-88 (for images see <*https://www.inaturalist.org/observations/12907271*>, <*https://www.inaturalist.org/observations/12771009*>). *Hermissenda opalescens* has therefore ranged to at least southern Oregon in the past, and *H. crassicornis* to at least the edge of the Southern California Bight, both likely as ephemeral range shifts driven by opposite phases of the El Niño Southern Oscillation (ENSO).

Hermosita hakunamatata (Ortea, Caballer and Espinosa, 2003). Punta Entrada, Isla Magdalena, Bahía Magdalena, Baja California Sur, Mexico, 3 specimens, with egg masses, on hydroid *Solanderia*, 2-5 m depth, 1 September 2015 (Fig. 3A) (observed by CH; also see Bertsch and Aguilar Rosas 2016) to Panama (Hermosillo 2004 [as *Phestilla hakunamatata*]).

Previous northernmost locality: Isla Isabella, Nayarit, Mexico (Hermosillo 2004).

Remarks: The specimens from Bahía Magdelena are the first record of *H. hakunamatata* from the Baja California peninsula. It was not recorded by Angulo-Campillo (2005) during his four year survey of opisthobranchs from Baja California Sur, including Bahía Magdelena.

Noumeaella rubrofasciata Gosliner, 1991. Outer Pinnacles, Carmel Bay, California, 1 specimen, 43 m depth, 4 March 2017 (C. Bauder, personal communication to JG, 5 March 2017; Bauder 2017) to Panama (Hermosillo 2004).

Previous northernmost locality: Malibu, California (Goddard et al. 2016).

Additional northern localities: Anacapa Island, California, 1 specimen, 12 m depth, north side of East Anacapa Is., 10 February 2018 (Klug 2018).

Phidiana hiltoni (O'Donoghue, 1927). Pinnacle Rock, Bodega Bay, Sonoma Co., California, 7 specimens, low rocky intertidal, 25 November 2015 (Sones 2015) to Cedros Island, Baja California, Mexico (Farmer and Collier 1963).

Previous northernmost locality: Palomarin, Marin Co., California (WP and DM, personal observations, January 2011); Duxbury Reef (Behrens 2004; and see Goddard et al. 2011).

Additional northern localities: Dillon Beach, Marin Co., California, low rocky intertidal, April 2014 – December 2017 (Thompson, 2017), and 8 specimens, 30 April 2017 (Fig. 3B) (observed by WP, DM, PD).

Remarks: *P. hiltoni* was first sighted in Bodega Bay at Pinnacle Rock in 2015, and 5 individuals were recorded during a survey on 4 December 2017 (JS and ES, personal observations). Thompson (2017) also recorded specimens from Dillon Beach, just 7 km south, in May, June, July, and December 2016, as well as in March, May, July, and August 2017, also indicating the persistence of this species in Bodega Bay following the initial sighting reported in 2015. Goddard et al. (2011, Appendix) compiled historical records of heterobranchs from Marin and Sonoma counties, which provide robust evidence for the historical absence of *P. hiltoni* in the region. Additional significant records can be extracted from Steinberg (1963) and Marcus (1961), with many of those records originating from the old Pacific Marine Station at Dillon Beach. Together, all of these

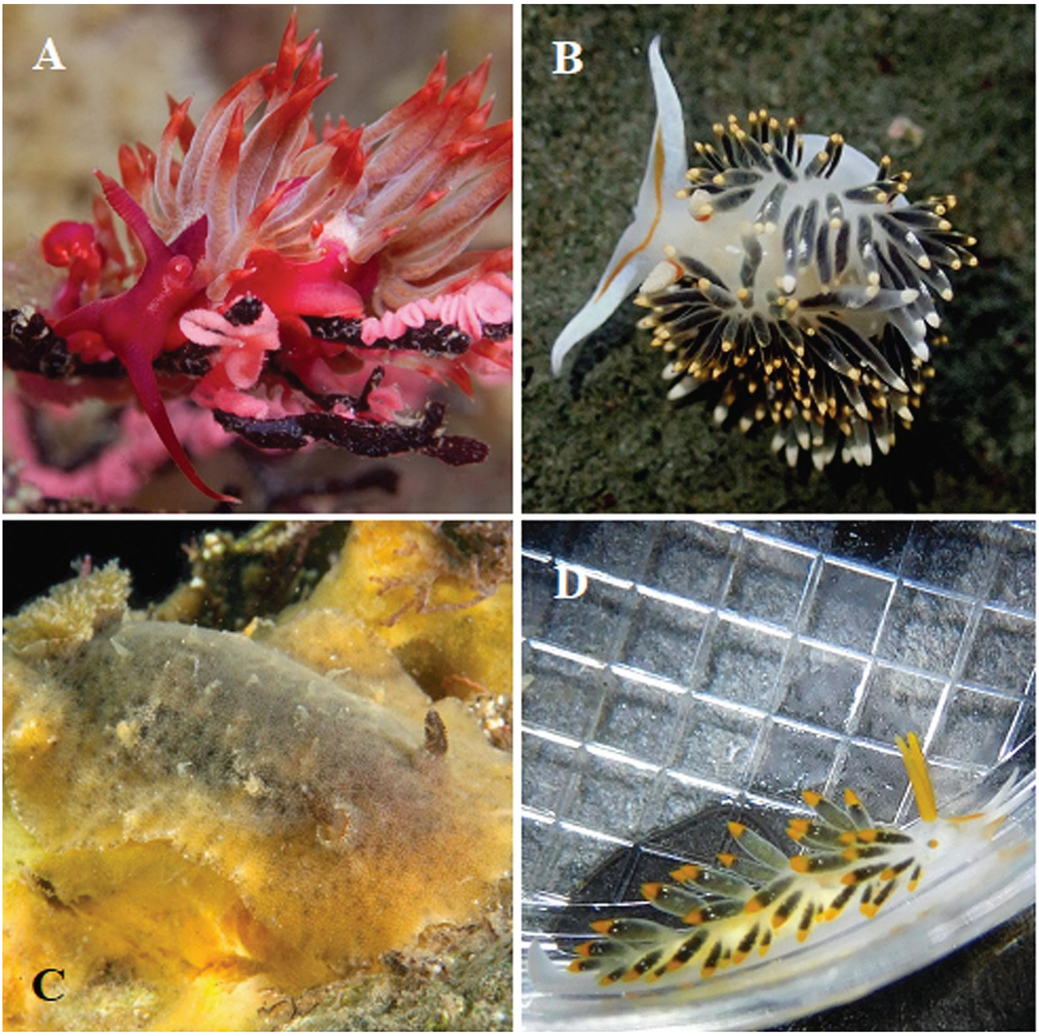

Figure 3. Nudibranch sea slugs found at new northern localities in the Northeastern Pacific Ocean, 2015–2017. **A** *Hermosita hakunamatata*, La Bocana, Bahía de Magdalena, Baja California Sur, Mexico, 1 September 2015. Image by CH. **B** *Phidiana hiltoni*, Dillon Beach, California, 30 April 2017. Image by DM. **C** *Taringa aivica*, Mission Bay, San Diego, California, 14 June 2018. Image by CH. **D** *Diaphoreolis lagunae*, Whiskey Creek, Curry Co., Oregon, 19 May 2017 (grid squares 2 mm on a side). Image by NT.

sources document the occurrence from the 1940s through 1970s of nearly 50 species of heterobranchs from the outer coast of northern Marin and Sonoma counties, and *Phidiana hiltoni* is not among them.

II. Additional species, at or near previous northernmost localities

In addition to the species listed above, 24 more were found in 2016 or 2017 at or near previously determined northernmost range limits. Four of these (*Aplysia californica*, *Aplysia vaccaria*, *Flabellina cooperi*, and *Flabellinopsis iodinea*) were found farther north in 2015–17 than in 2014–15 as reported by Goddard et al. (2016), and are documented individually below, along

TABLE 2. Species included in Goddard et al. (2016) that were found in 2016–17 at or near, but not beyond, previously determined northern range limits. The relevant observation(s) can be found by searching by species the websites given in the right column. Initials in the right column refer to authors of the present study.

Species	Site(s)	Source
Navanax inermis (Cooper, 1863)	Bodega Harbor, Tomales Bay, Drake's Estero, CA	iNaturalist
Okenia rosacea (MacFarland, 1905)	Cape Arago, OR	iNaturalist
Thordisa bimaculata Lance, 1966	Monterey Peninsula	Observations by BG on iNaturalist
Felimare californiensis (Bergh, 1879)	Anacapa & Santa Cruz Islands, CA	"divindk" [D. Klug] on Flickr
Felimida macfarlandi (Cockerell, 1901)	Monterey, CA	Observations by BG, RA, & others on iNaturalist
Janolus anulatus Camacho-García & Gosliner, 2006	Tarpits Reef, Carpinteria, CA	Observations by JG on iNaturalist
Janolus barbarensis (Cooper, 1863)	San Francisco Bay, CA	iNaturalist
Anteaeolidiella oliviae (MacFarland, 1966)	Sonoma coast, CA	iNaturalist
Babakina festiva (Roller, 1972)	Fitzgerald Marine Reserve, CA	iNaturalist
Cuthona phoenix Gosliner, 1981	Monterey, CA	Observations by RA on iNaturalist

with 10 more species not included in Goddard et al. (2016). The remaining 10 species are listed in Table 2.

Bulla gouldiana (Pilsbry, 1893). Elkhorn Slough, 1 specimen, intertidal mud flats, 16 May 2018 (Imkitayama 2018b). Morro Bay, California, intertidal muddy sand flats, May through mid-November 2017 (observed by JG; for image see <*https://www.inaturalist.org/observations/3127748*>; Eaton 2016). On 13 November 2016 shells measured up to 50 mm long, and one yellow egg string was found (see <*https://www.inaturalist.org/observations/6223507*>). Bentall (2017) noted only large, empty shells at one site in Morro Bay in March 2017, but in November 2017 JG observed numerous large specimens and their egg strings (see <*https://www.inaturalist.org/observations/8818733*>).

Remarks: The published northern limit of *B. gouldiana* is Morro Bay (Roller and Long 1969; Behrens and Hermosillo 2005). However, *Bulla gouldiana* was also recorded as uncommon on Bodega tide flats in a list of marine invertebrates from Sonoma Co. compiled by Victor Chow in 2013 (see <*http://bml.ucdavis.edu/bmr/invert_list.PDF*>). Additionally, Moss Landing Marine Laboratories (MLML) has in its Invertebrate Collection a preserved specimen (Catalogue No. MO600) collected from mudflats near the mouth of Elkhorn Slough in Monterey Bay (see <*http://digital.mlml.calstate.edu/islandora/object/islandora%3A15334*>). No collection date is given, but the specimen was identified by John Cooper, who was a graduate student at MLML in the 1970s. This specimen presumably forms the basis for the inclusion of *B. gouldiana* in species lists for Elkhorn Slough available in technical reports (e.g., DeVogelaere et al. 1998).

At Naples, an open coast site on the south coast of Santa Barbara Co., *B. gouldiana* was absent from 2006 until late 2015, reached high adult densities by winter 2016, laid egg strings in May and June 2016, was absent by September 2016, and, in contrast to the population in Morro Bay, has not been observed again through mid-2018 (Fig. 4).

Aplysia californica (Cooper, 1863). Yaquina Bay, Oregon, August 2016; one large specimen was found in a water storage reservoir, filled from Yaquina Bay, used by the Oregon Coast Aquarium (Pearsall 2016).

Remarks: The specimen noted above was most likely pumped into the reservoir as a free-swimming veliger larva. *Aplysia californica* has been reported from as far north as Yaquina Bay once before, during the strong 1982-83 El Niño (Pearcy and Schoener 1987).

Aplysia vaccaria Winckler, 1955. Elkhorn Slough, Monterey Bay, California, at least 2 specimens and egg strings, low rocky intertidal, 8 July 2016 (Blue Water Ventures 2016); at least 1 specimen, "low tide," 16 May 2018 (Imkitayama 2018a).

Remarks: Behrens (1991) first reported *Aplysia vaccaria* from Monterey Bay but did not specify a precise locality. Therefore the above observations from Elkhorn Slough might represent a small northward range extension from Monterey, where *A. vaccaria* was found in December 2014 (RA, personal observations, for image see <*https://www.inaturalist.org/observations/1132630*>), September and October 2015 (Goddard et al. 2016; BG personal observations, for image see <*https://www.inaturalist.org/observations/5181629*>).

Aplysia vaccaria is usually found south of the Palos Verdes Peninsula (JG, personal observations). At Naples, Santa Barbara Co., it appeared briefly in late 2013 and again in late 2014, but then appeared in abundance starting in mid-2016, laid egg strings in October 2016 and April, October and November 2017 (JG, personal observations), and has persisted through 2017 (Figure 4).

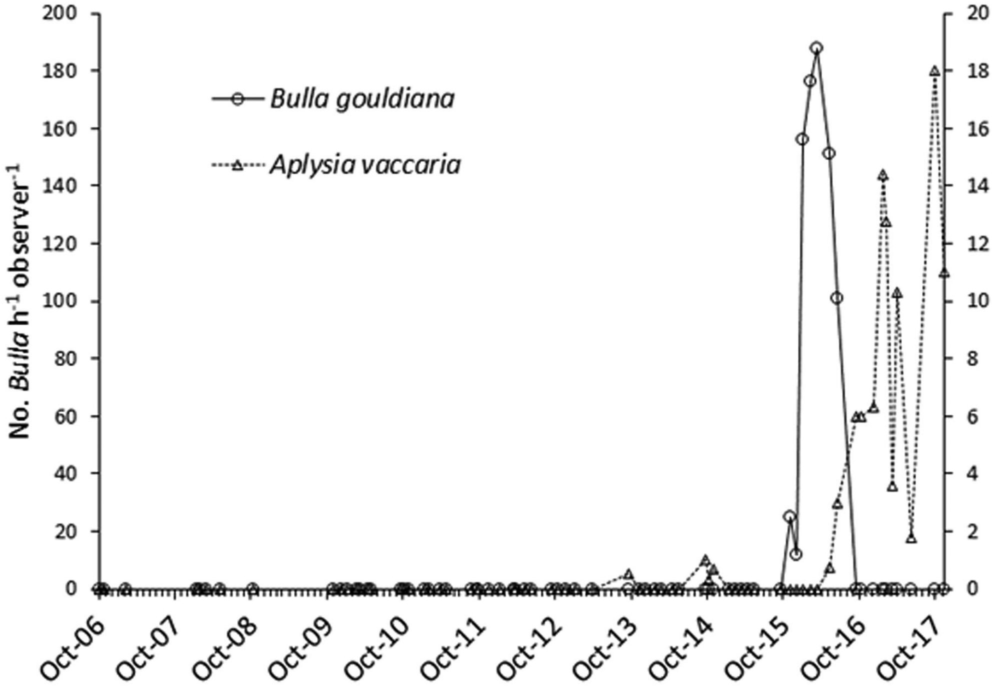

FIGURE 4. Abundance of the *Bulla gouldiana* and *Aplysia vaccaria* in the low rocky intertidal at Naples, Santa Barbara, California 2006–2017.

Berthellina ilisima (Ev. Marcus and Er. Marcus, 1967). Ellwood Mesa Reef, 1 specimen, 13 m depth, 2 November 2016; 3 specimens, 13 m depth, 11 January 2017 (C. Pierre, personal communication to JG, 6 October 2016). Living specimens were held at the Marine Science Institute, UCSB, and observed by JG, 6 October 2017. Anacapa Is, 1 specimen, intertidal, 22 May 2018 (Taylor 2018).

Remarks: *Berthellina ilisima* was reported from Naples Reef by Behrens (1991 [as *B. engeli*]), where it was found again by Shane Anderson of UCSB in October 1999, collected, and its development to hatching documented by Goddard and Hermosillo (2008).

Polycera alabe Collier and Farmer, 1964. Anacapa Island, California, 1 specimen, 23 m depth, north side of West Is., 18 December 2015 (D. Klug, personal communication to JG, 24 January 2016; for image see Klug 2015).

Remarks: The specimen observed by Klug (2015) matches variation A pictured by Behrens and Hermosillo (2005) and Hermosillo et al. (2006) and considered to be *P. alabe* by Pola et al. (2014). It was found 4.5 km west of Cathedral Cove, on the north side of East Anacapa Island, where one specimen of *P. alabe* was found during the 1997-98 El Niño (Engle and Richards 2001).

Atagema alba (O'Donoghue, 1927). Monterey Breakwater, Monterey, California, 1 specimen, 6 m depth, 20 August 2016 (P. Webster, personal communication to JG, with image, 23 August 2016). Carmel Point, Carmel, California, 1 specimen, 45 mm long, low rocky intertidal, 27 June 2017 (observed by JG; for image see <*https://www.inaturalist.org/observations/6834885*>).

Remarks: MacFarland (1966) reported the collection of 4 specimens of this species (as *Petelodoris spongicola* MacFarland, new species) from the Monterey Peninsula in 1908.

Aldisa sanguinea (Cooper, 1863), Otter Crest, Oregon, 2 specimens, under low rocky intertidal ledges, 3 June 2016 (observed by JG).

Remarks: Each of the above specimens were red and had two spots on the middle of the dorsum. Goddard (1997) reported finding 3 specimens of *A. sanguinea* at Otter Crest, which was the northernmost locality for the species until specimens were reported from Campbell River, on the east coast of Vancouver Island and Scott's Bay, Barkley Sound, on the west coast of Vancouver Island, British Columbia by Wakeling (2005) and Penney (2005), respectively.

Baptodoris mimetica Gosliner, 1991. Carmel Point, California, 1 specimen, low rocky intertidal 27 June 2017 (observed by JG; for image see <*https://www.inaturalist.org/observations/6834892*>).

Remarks: The published northern limit for this species is Santa Cruz, California (Gosliner 1991). However JG found one specimen in the low rocky intertidal at Salt Point, Sonoma Co., California in July 2010; for image see <*https://www.inaturalist.org/observations/2941658*>.

Jorunna pardus Behrens and Henderson, 1981. Anacapa Island, California, 1 specimen, subtidal, off the west end of the West Anacapa, 7 October 2016 (Klug 2016b), and 1 specimen, subtidal, off the north side of Middle Anacapa, 29 December 2016 (Klug 2016c).

Remarks: Behrens and Henderson (1981) noted 7 specimens from Anacapa Island, which has remained the northernmost known locality for this species.

Taringa aivica Ev. Marcus and Er. Marcus, 1967. La Jolla Shores, California, 1 specimen found by John Huber at an unspecified depth, 8 August 2016 (Doyle 2016). Mission Bay, San Diego, California, 1 specimen, 2 m depth, 14 June 2018 (Fig. 3C) (observed by CH).

Remarks: These are the first documented sightings of this Panamic species in the Southern California Bight since Behrens and Henderson (1982) reported finding a single specimen at 10 m depth in Paradise Cove, Malibu in April 1979. Paradise Cove remains the northernmost known locality for *T. aivica*.

Felimare porterae (Cockerell, 1901). Pacific Grove, Monterey Co., California, 1 specimen, subtidal, 27 June 2017 (Gerakin 2017). Carmel Pinnacles, Monterey Co., California, 2 specimens, 46 m depth, 24 September 2016 (C. Bauder, personal communication to JG 29 September 2016; for image see <*http://www.baue.org/images/galleries/v/local/Lunaticos_9-24-16/*>). Point Sierra Nevada, San Luis Obispo Co., California, 1 specimen, 29 January 2018 (observed by JG; see <*https://www.inaturalist.org/observations/9698537*>). Near Point Buchon, San Luis Obispo Co., California, 1 specimen [as *Mexichromis porterae*], subtidal, 29 July 2016 (Harmer 2016). Cave Landing, San Luis Obispo Co., California, 1 specimen, 17 mm long crawling, 4 December 2017 (observed by JG; for image see <*https://www.inaturalist.org/observations/9057952*>).

Remarks: *Felimare porterae* was found on the Monterey Peninsula for the first time in 1894 (MacFarland 1905 [as *Chromodoris porterae*]). It has been found only a few times in that area since (MacFarland 1966; GM, personal observations; for image see <*https://www.inaturalist.org/observations/845636*>), and has not been reported from farther north. Additionally, Harmer's (2016) image represents only the second time *F. porterae* has been found in San Luis Obispo Co., the first was during subtidal monitoring conducted from 1976 to 2001 as part of studies on the effects of the thermal discharge by the nuclear power plant at Diablo Canyon, (D. Behrens, personal communication, with unpublished manuscript, to JG, 29 January 2006; also see Steinbeck et al. 2005). *Felimare porterae* is a Californian species usually found south of the Palos Verdes peninsula.

Diaphoreolis lagunae (O'Donoghue, 1926). Whiskey Creek, Curry Co., Oregon, low rocky intertidal, 2 specimens, 16 June 2015 (observed by JG et al.), and 1 specimen (Fig. 3D), 29 May 2017 (observed by NT).

Remarks: *Diaphoreolis lagunae* has been recorded previously in Oregon only three times, twice (July 1987 and June 1995) from Whiskey Creek (Goddard 1990, 1991 [as *Cuthona lagunae*], personal observations) during strong and moderate El Niño events, respectively, and once (June 1996) from 48 km north in the low rocky intertidal on the south side of Humbug Mountain (Goddard 1997, CASIZ 107440) during a weak La Niña following a moderate El Niño. Goddard (1991, p. 152) also recorded one specimen from the low rocky intertidal near Crescent City, California in July 1998, during the strong 1997-98 El Niño.

Flabellina cooperi (Cockerell, 1901). Fitzgerald Marine Reserve, San Mateo Co., California, low rocky intertidal, 1 specimen, 20 June 2016 (observed by RA; for image see <*https://www.inaturalist.org/observations/3492678*>).

Remarks: *Flabellina cooperi* is known as far north as Coleman Beach, Sonoma Co., California (Goddard et al. 2016)

Flabellinopsis iodinea (Cooper, 1863). Cape Flattery, Washington, subtidal, At least 10 specimens observed and photographed by Karin Fletcher and Doug Miller on 6 dates, August 2015 (Pacific Northwest Shell Club 2016 [as *Flabellina iodinea*]).

Remarks: *Flabellinopsis iodinea* has been found north to Vancouver Island, British Columbia (Bernard 1970; and see Goddard et al. 2016)

Discussion

During and in the two years following the 2015–16 El Niño 37 species of heterobranch sea slugs were recorded north of their usual ranges, a total similar to the 30 total listed by Goddard et al. (2016) for the 2014-15 warm anomaly in the Northeast Pacific Ocean. However, the 23 species found at new northernmost localities in the current study and Merlo et al. (2018) is more than double the number reported by Goddard et al. (2016), and their mean range extension was 270 km, or 79% longer. While taxonomic splits since 2016 (Lindsay and Valdés 2016; Uribe et al 2017) account for the addition of two species (*Limacia mcdonaldi* and *Hermissenda opalescens*) to the recent total, the 2015-16 El Niño clearly had a significant effect on heterobranch distributions in the region.

Of the 37 species treated herein, 22 were not among the species covered by Goddard et al. (2016). The combined 2014–17 marine heat wave in the Northeast Pacific Ocean therefore drove range shifts in at least 52 species of benthic heterobranchs, approximately one quarter of the species known from the Californian and Oregonian biogeographic provinces (Behrens and Hermosillo 2005). Thirty of the 52 were found farther north than ever observed before. Although clearly significant and likely unprecedented, it is difficult to directly compare these numbers to those observed during warm-water events of the last half century, owing to (1) historical gaps in sampling coverage, (2) lack of dates for some of the earlier records, (3) recent taxonomic revisions, and (4) increased numbers of observers, especially citizen scientists, combined with increased opportunities for posting online geo-referenced observations accompanied by images. As evidenced by the number of known northern range limits that were not surpassed by species we found in our studies, many have been advected as larvae and settled as far north before, especially during strong El Niño events. These include, for example, *Bulla gouldiana*, *Aplysia californica*, *Berthellina ilisima*, *Polycera alabe*, *Dirona picta*, the chromodorids *Felimare porterae* and *Felimida macfarlandi*, and *Flabellinopsis iodinea* (Goddard et al. 2016; present study and references therein). However, the range shifts since late 2013 by species like *Okenia rosacea*, *Carminodoris bramale*, *Doriopsilla fulva*, *Anteaeolidiella oliviae*, *Noumeaella rubrofasciata*, and *Phidiana hiltoni* are unprecedented, either in geographic extent or population density, with their prior absence from new northern ranges backed by historical records.

The sheer number of heterobranch range shifts associated with the 2014–17 marine heat wave, especially those to new northernmost localities, begs questions about the possible role of global warming, beyond simple temperature increases in the California Current System and Northeast Pacific, which so far have been less than in other ocean regions (Cheng et al. 2017). Disproportionate Arctic warming, or “Arctic amplification,” has been implicated in slowing the Northern Hemisphere polar jet stream, making it wavier, with more persistent high pressure ridges and low pressure troughs (Francis and Vavrus 2015; Francis et al. 2017). This increased amplitude and persistence is reflected in the North Pacific Oscillation (NPO), a leading pattern of atmospheric variability. A persistent atmospheric ridge was observed over the Northeast Pacific during winter 2013-2014, which by altering wind stress and reducing the depth of the mixed layer generated the 2014 warm anomaly in sea-surface temperatures (Bond et al. 2015). Atmospheric teleconnections between the North Pacific and tropical Pacific and back again are then thought to have effectively forced phase changes in the Northeast Pacific reflected first in the North Pacific Gyre Oscillation (NPGO), then the Pacific Decadal Oscillation (PDO), and ultimately the El Niño Southern Oscillation (ENSO) (Di Lorenzo and Mantua 2016; and see Levine and McPhaden 2016). The direction of the observed phase changes are known to be associated with, among other effects, reduced coastal upwelling and increased poleward and onshore transport of coastal waters in the NE Pacific, which can advect planktonic propagules and pelagic organisms poleward, well beyond their usual ranges (e.g., Lluch-Belda et al. 2005; Ohman et al. 2017). Global warming, by increasing the amplitude and persistence of the NPO, therefore appears to be important in driving increased poleward range shifts. The unprecedented magnitude and duration of the 2014–17 marine heat wave likely also contributed to the continued presence at outer coast sites of recently arrived southern heterobranchs such as *Okenia rosacea*, *Doriopsilla fulva,* and *Hermissenda opalescens* in Oregon and *Phidiana hiltoni* in northern California by keeping open thermal windows conducive to growth, reproduction and development.

At Naples, an outer coast site in the northern part of the Southern California Bight, *Bulla gouldiana* was present for about one year after first appearing (Figure 4), while to the north at Morro Bay, *B. gouldiana* continues to be present after at least two years. Southern species may persist longer in embayments compared to nearby outer coast sites, owing to elevated summer temperatures on the one hand, and increased potential for larval retention and local recruitment on the other, thus allowing for reproduction and completion of life cycles in the bays. With the return to ENSO-neutral conditions and more normal sea-surface temperatures in the NE Pacific Ocean, it will be interesting to see how long southern species like *Bulla gouldiana*, *Aplysia californica*, *A. vaccaria*, and *Doriopsilla fulva* persist in northern embayments.

Site-specific topography aside, with global ocean temperatures steadily increasing in the background, recently settled southern species are likely to persist longer in their recently expanded northern ranges, especially compared to historically more ephemeral ENSO-driven range shifts (reviewed by Lluch-Belda et al. 2005). So far this appears to be the case for *Okenia rosacea*, *Doriopsilla fulva*, *D. gemela*, *Felimida macfarlandi*, *Doto* form A, *Janolus anulatus*, and *Fla-bellina cooperi*, all of which were found in 2017 at or near range limits reached a year or two earlier (Goddard et al. 2016; present study). However, other range shifts documented by Goddard et al. (2016) appear to have been short-lived, with no northern sightings since 2015 of *Placida brookae* McCarthy, Krug and Valdés 2017 (formerly *P. cremoniana*), *Trapania velox*, *Hancockia californica* MacFarland, 1923, *Anteaeolidiella chromosoma* (Cockerell and Eliot, 1905), and *Emarcusia morroensis* Roller, 1972. *Phidiana hiltoni*, which has been taking smaller geographic steps with its lecithotrophic larvae, has yet to retreat from any new range acquired since 1977 and remains the best documented example of a permanent northern range shift among Northeast Pacific heterobranchs (Goddard et al. 2011; present study; King et al. in prep).

In central California southward range shifts by nudibranchs with more northern distributions were last observed during the strong La Niña events of 2007–08 and 2010–11 (e.g., *Aldisa albomarginata* Millen in Millen and Gosliner, 1985, *Aldisa cooperi*, Robilliard and Baba, 1972, *Diaulula lentiginosa* (Millen, 1982), and *Doris odhneri* (MacFarland, 1966) subtidally off the Monterey Peninsula [see records at <*http://www.baue.org/images/galleries/v/FieldGuide/Opistho branchs/*>], and *Janolus fuscus* (O'Donoghue, 1924) intertidally in San Luis Obispo Co. [JG personal observations, CASIZ 186479]). We did not observe any southern range shifts during the 2014–17 marine heat wave, and the only record of a more northerly species penetrating central California we are aware of during this period is of *Dirona albolineata* MacFarland in Cockerell and Eliot, 1905 at Pillar Point (<*https://www.inaturalist.org/observations/1727582*>). The last time *D. albolineata* was recorded farther south was during the 2009–10 La Niña, by GM at Carmel Point, on the Monterey Peninsula (for image see <*https://www.inaturalist.org/observations/834800*>).

As the oceans continue to warm we expect more poleward range shifts by heterobranchs to become permanent, and likely lead to complex and unexpected changes in shallow-water benthic encrusting and fouling communities.

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Redescription of the Holotype of *Argulus floridensis* Meehean, 1940 (Arthropoda, Crustacea, Argulidae)

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The holotype male of *Argulus floridensis* Meehean, 1940 is redescribed and illustrated in greater detail to provide new morphological and meristic information that will aid in identification of other specimens.

KEYWORDS: Crustacea, Branchiura, Argulidae, morphology, taxonomy

Meehean (1940) revised the taxonomy of the *Argulus* spp. in the National Museum of Natural History and included a description of one new species, *Argulus floridensis*. Only a single male, previously identified as *A. pugettensis* Dana, 1853, was available at the time. Meehean (1940, p. 489) noted that the specimen was in poor condition; it has continued to deteriorate and now is in very poor condition. Both carapace alae have disintegrated, and the posterior respiratory areas cannot be found now. The left first maxilla is missing. Basal segments of the legs remain intact, and the abdomen is in good condition. Illustrations were made of the right second maxilla, left antennae, two rods from the right first maxilla, the abdomen and fleshy lobe at posterior of thorax, and the second, third, and fourth legs on the left side, showing the secondary sexual modifications (right and left from dorsal view of specimen). Meehean (1940) illustrated the right second and fourth legs and the left third leg. My illustrations and observations of the legs generally agree with those of Meehean, except for the inclusion of more details and additional features, which will be mentioned below, that were not in the original description.

In his last work on Branchiura and Copepoda, Wilson (1944) included characters of *A. floridensis* in a key to *Argulus* spp., but did not add any new details to Meehean's original description. Cressey (1972) included *A. floridensis* in a key to species, but no additional morphological information was provided. In the list of figures, *A. floridensis* was included under basal plates of second maxilla (Cressey 1972, p. viii); however, no illustration for *A. floridensis* was in that figure. Cressey (1972) listed one host, *Mugil* sp. (mullet), for *A. floridensis*, but that information is erroneous (W. Poly pers. obs.). A thorough redescription of the species must wait until collections are available that include a good series of males and females. The purpose of this redescription of the holotype is to make available new details of the male such that others, who might already possess specimens or who might collect some in the future, will be able to identify them as *A. floridensis*.

MATERIALS AND METHODS

The holotype was examined as a temporary slide mount (with 70% ethanol and Hoyer's medium), and drawings were made with the aid of a camera lucida (Poly 2016).

Results

Family Argulidae Rafinesque, 1815

Argulus Müller, 1785

Argulus floridensis Meehean, 1940
Florida fishlouse Figures 1–6.

Material examined.— Holotype (unique), adult male, 5.46 mm total length [Meehean 1940: 5.85 mm], USNM 77810 [see note], Key West, Florida, 1884, collector: A.E. Verrill [= Addison Emery Verrill]. Note: Meehean (1940, p. 467) listed the catalog number as "77810 (old number 60589);" mentioned here in case of relevant information in historical records under the old number.

Diagnosis.— Two respiratory areas with smaller oblong "area" anterior to slightly larger oblong posterior "area;" single postantennal spines very broad; male with 77 support rods in suction cup; 14–19 sclerites per rod in male; mouth tube with at least 19 scales on basal half; basal plate of second maxilla with 3 stout spines, scales covering nearly entire raised pad, one stout, naked seta on posterior margin of pad; accessory spines on thorax large, very broad base on raised pad with many scales, tapering to rounded tips; first 2 pairs of legs lacking flagella; posteroventral surface of coxae of second legs of male expanded into a broadly-rounded lobe that is covered with many small and closely-arranged scales; third legs of male with two pegs issuing from cleft on dorsal side of legs and two fingerlike papillae; small fleshy lobe at posterior of thorax; male abdomen bilobate with testes extending to the level of the anal sinus base; caudal rami long, slender, basal in anal sinus.

Description.— Total length 5.46 mm [Meehean 1940: 5.85 mm]. Carapace shape is "ovate, sinuses shallow, cephalic areas broad...; alae reaching abdomen [Meehean 1940]." Carapace length [Meehean 1940: 4.88 mm]. Maximum carapace width [Meehean 1940: 4.28 mm]. Pair of compound eyes anteriorly with diameters 250 (left) and 220 (right) µm. Transverse distance between eyes 0.83 mm (830 µm). Nauplius eye with one anterior and two posterior ocelli. Sclerotized dorsal ridges not forked anterior of eyes. Ventrally, carapace with small, posteriorly-projecting spines along outer margin [due to the deteriorated condition of the carapace alae, additional details cannot be included here]. Respiratory areas consist of two oblong-shaped areas, anterior one slightly smaller than posterior [from Meehean 1940] (Fig. 1). No pigmentation present (but probably lost in preservative and/or due to clearing).

Thorax compressed dorsoventrally, 4-segmented, with 2 pairs of posteriorly-projecting spines ventrally. Spines digitate with broad base, anterior pair (accessory spines) larger than posterior pair (postmaxillary spines), both pairs angled mesially. Accessory spines between basal segments of second maxillae; very broad base on a raised pad covered with many scales; spines tapering to rounded tips (Fig. 2). Male with ovoid fleshy lobe at posterior of fourth thoracic segment between natatory lobes (Figs. 3A, 4). Thorax with scales scattered on ventral surface; thoracic segment at base of third leg produced laterally into expanded anterolateral lobe with scales

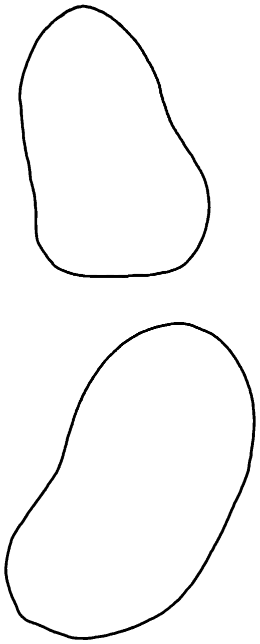

Figure 1. *Argulus floridensis*: shape of anterior and posterior respiratory areas (redrawn from Meehean 1940).

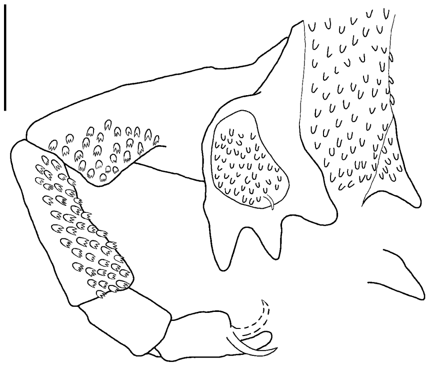

FIGURE 2. *Argulus floridensis*: Second maxilla, raised pad with scales (adjacent on thorax), accessory spine, and postmaxillary spine. Scale bar = 200 µm.

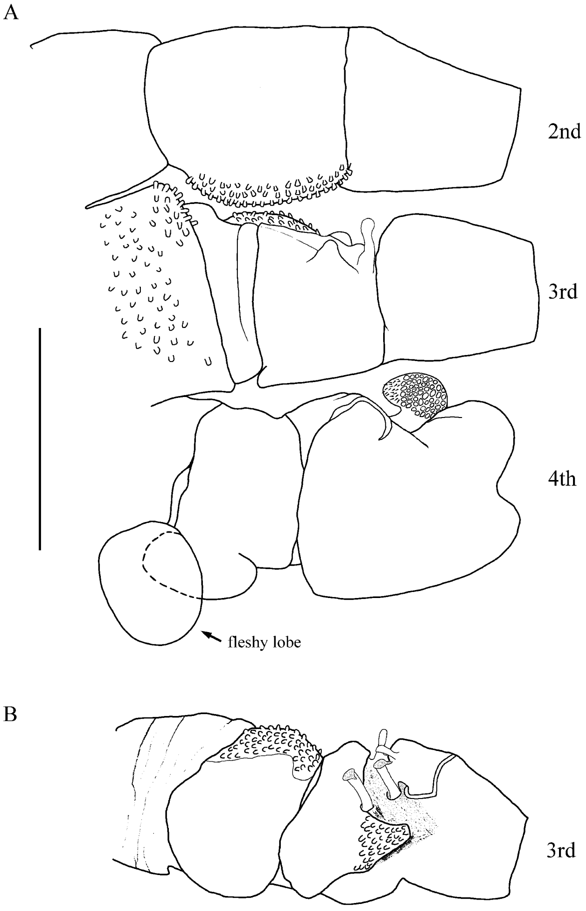

FIGURE 3. *Argulus floridensis*: A) ventral view of legs 2, 3, and 4 (precoxa, coxa, and basis only); exopods, endopods, setae, and sensillae omitted. B) dorsal view of leg 3 (precoxa, coxa, and basis only). Scale bar = 500 µm.

protruding laterally and anteriorly in apposition to posterior lobe of coxae of second legs (Fig. 3A). Four pairs of biramous swimming legs composed of a precoxa, coxa, basis, exopod, and endopod. Exopods and endopods with plumose setae. First two pairs of legs lacking flagella. Endopods of first pair of legs 3-segmented with 3 setae distally. Endopods of second pair of legs unsegmented. Endopods of third and fourth pairs of legs 2-segmented. Second, third, and fourth legs of male with secondary sexual structures (Figs. 3A, B).

First legs lack secondary modifications. Second legs, the posterior ventral margin of coxae expanded into broadly-rounded lobe with many small, closely-arranged scales. Third legs, dorsal anterior coxae with broadly-rounded hump armed with many scales directed proximally; distal to this hump are two smaller, unarmed protuberances; at anterior distal margin of coxae an anteriorly-directed, fleshy projection ("upright fingerlike papilla" of Meehean 1940) (Fig. 3A).

Third legs with two sclerotized pegs in cleft on dorsal side at distal margins of coxae (or fused coxae+bases); pegs with a single, large horn and orifice distally; sclerotized ridge at anterior dorsal of coxa/basis junction; one fleshy papilla extends proximally (mesially) from sclerotized ridge anterior of two pegs and overhanging cleft ("saddle-shaped depression" of Meehean 1940). Posterior to pegs and cleft a triangular-shaped lobe covered with scales (Fig. 3B). Posterior margins of both precoxae+coxae and bases of fourth legs with natatory lobes bearing plumose setae. Anterior of bases a sclerotized ridge lies on basal half, opposed by recurved, finger-like appendage covered with fine scales distally; tiny spines or scales on its tip (Fig. 3A).

Abdomen bilobate. Abdomen length 1.72 mm [Meehean 1940: 1.58 mm]; maximum width

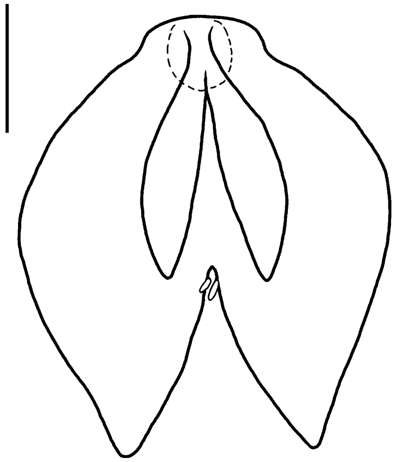

FIGURE 4. *Argulus floridensis*: abdomen; fleshy lobe at posterior of thorax is shown as a dashed outline at anterior of abdomen. Setae not shown on caudal rami. Scale bar = 500 µm.

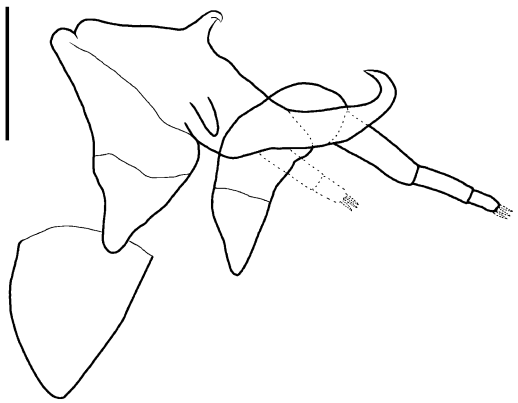

FIGURE 5. *Argulus floridensis*: first and second antennae. The fleshy segments of the first antennae were obscured or missing on this structure but are included as dashed outlines. Scale bar = 200 µm.

1.44 mm [Meehean 1940: 1.35 mm]. Anal sinus length 0.72 mm (720 µm) [Meehean 1940: 0.98 mm]. Caudal rami paired, long, slender, near base of anal sinus (could not see the setae clearly, usually there are 5 simple setae at the tip of each). Tips of abdominal lobes narrowly rounded, not pointy. Testes extending to level of anal sinus base (Fig. 4). Scales absent on ventral surface of abdomen; spines or scales absent along margins of abdominal lobes.

Mouth tube long, slender, with at least 19 scales on basal half.

First antennae 4-segmented. First segment (basal segment) sclerotized, large with stout posteriorly-projecting posterior spine, narrowly rounded at tip; second segment sclerotized with small recurved spine anteriorly with narrow, blunt tip, posteriorly-projecting medial spine with rounded tip, and large recurved terminal spine; third and fourth fleshy segments missing or obscured on the holotype (Fig. 5). Width of first antennae (mean of both antennae, µm) 530–540 (535) in male. Second antennae 5-segmented, fleshy. First two segments larger; remaining three thin, cylindrical; basal segment bears posteriorly-projecting posterior spine with narrowly-rounded tip. Postantennal spines single (as opposed to double in some taxa), very wide at base, tapering to narrowly-rounded tip (Fig. 5).

First maxillae modified into suction cups in adult. In male, first maxillae inner diameter 680 µm and outer diameter 1,050 µm (n = 1). Number of sclerites per support rod in male 14–19 (n = 25 support rods) [excludes abnormal rods with missing sclerites]. Basal (proximal) sclerite usually subquadrangular, shape variable; distal sclerites imbricate bowls, plates (Fig. 6). Suction cup with 29 sensilla on inside circumference.

Second maxillae 5-segmented with broad basal plate bearing three stout spines with the mesial spine broader than the other two (Fig. 2). Basal plate with elevated pad bearing 43 scales and one stout seta posteriorly. Bi-dentate to multidentate scales on ventral surfaces of segments 2 and 3; segment 4 lacking armature. Distal segment with

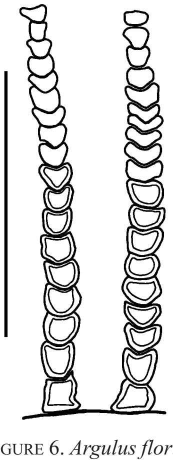

FIGURE 6. *Argulus floridensis*: Two support rods from suction cup (right first maxilla), Scale bar = 100 µm,

2 sharp claws (1 broken/missing) and one blunt, elongate lobe positioned above claws (did not see a small sensillum at tip of lobe).

HOST.— Unknown.

ETYMOLOGY.— The specific name, *floridensis*, is derived from the state, Florida, in which the type locality is located and has an adjectival suffix, ensis, meaning "of or from Florida."

DISCUSSION

Not mentioned in the earlier description is that the third thoracic segment is produced laterally into an expanded anterolateral lobe that has scales protruding laterally and anteriorly in apposition to the posterior lobe of the coxae of the second legs. The fleshy lobe at posterior of thorax, the fleshy papilla and sclerotized pegs on the dorsal side of the third legs, number of support rods, and other measurements and morphological details also were not included in the original description. Meehean's description of a "broadly bilobed lamella" applies to the right second leg on which the lobe does have a slight indentation or wrinkle near its midpoint. This demonstrates how slight differences can exist in structures within a species and even on the same specimen. Additional specimens are needed to determine if both conditions occur normally or if one might be abnormal or an artifact of preservation (the present author believes the morphology shown in Fig. 3A is likely the normal condition).

Of the 10 *Argulus* spp. reported from the Gulf of Mexico region in Poly (2009), the number of sclerites in the suction cup support rods of *A. floridensis* exceeds that of eight of the other species, with *A. funduli* being the only exception; the holotype (male) of *A. floridensis* has 14–19 sclerites per support rod compared with *A. funduli* (11–21, male; 12–26 female), *A. fuscus* Bere, 1936 (6–7, male; 12–14, female), *A. alosae* Gould, 1841 (10–12), *A. rotundus* Wilson, 1944 (11), *A. yucatanus* Poly, 2005 (2–5), *A. laticauda* Smith, 1873 (3–4), *A. megalops* Smith, 1873 (5–10), *A. varians* Bere, 1936 (3–6), *A. bicolor* Bere, 1936 (6–10) (Bere 1936; Meehean 1940; Wilson 1944; Cressey 1972; Bouchet 1985; Poly 2005). However, male *A. funduli* lack secondary sexual modifications on the second legs, lack accessory spines and postmaxillary spines, have short, blunt teeth on the basal plate of the second maxilla, and have a long thin abdomen that has many scales on its ventral surface (Poly, 2005, unpubl. data). The holotype of *A. floridensis* has 77 support rods in the first maxilla (suction cup) compared with *A. yucatanus* (37– 51), *A. funduli* (53–64), *A. cubensis* (39–49), and *A. chromidis* (42). Unfortunately, numbers of support rods for nearly all *Argulus* spp. were never reported in original descriptions or subsequent studies but should be included as it is a valuable meristic character. Structures on the bases of the fourth legs of *A. floridensis*, *A. kosus* Avenant-Oldewage, 1994, and *A. yucatanus* are very similar, and males of these three species also have a fleshy lobe on the posterior margin of the thorax between the coxae of the fourth legs. However, features of the first and second maxillae and secondary sexual structures on legs of males distinguish among these three species (Van As et al. 1999; Poly 2005). The pair of pegs on the third legs of male *A. floridensis* resemble structures on males of other species, including *A. arcassonensis* Cuénot, 1912, *A. kusafugu* Yamaguti and Yamasu, 1959, *A. kosus*, and *A. yucatanus* (Yamaguti and Yamasu 1959; Masson and Delamare Deboutteville 1963; Van As et al. 1999; Poly 2005).

Argulus floridensis requires a more thorough redescription based on a good sample of male and females specimens and including more meristic and morphometric information such as numbers of suction cup support rods, types and numbers of scales on various structures, setae, sensillae, and other details. Illustrations of additional structures and inclusion of more details of the holotype herein should allow for identification of other specimens of *Argulus floridensis*.

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